Role of cephalopods in the structure and functioning of marine ecosystems.

By

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Submitted in fulfilment of the requirements for the Doctor of Philosophy

University of Tasmania May, 2019

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Statement of Co-Authorship

One chapter is under revision in a peer-reviewed journal:

Thibaut de la Chesnais , Elizabeth A. Fulton, Sean R. Tracey, Gretta T. Pecl (in review) The ecological role of cephalopods and their representation in ecosystem models.

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Abstract

An increase in cephalopod abundance worldwide has been observed over recent decades, possibly a function of cephalopods' response to the effects of climate change and the reduction in predation by human exploitation on predators of marine systems. Additionally, there has been a renewal of fisheries interest due to the development of markets for cephalopod products and the reduction of finfish stocks. Assessing their role in food webs is thus essential for understanding and anticipating upcoming changes in ecosystem functioning and services. From this perspective, ecosystem models can be used as powerful tools to understand the impact of a group of species on the system, and to anticipate future developments and foresee the future dynamics. However, these models generally fail to represent cephalopods ecology adequately. This thesis thus aimed to tackle the issue of representing cephalopods ecology in ecosystem models and to use these new methods to assess their role in ecosystems and the potential changing of this role under climate change:

- Identifying the limits of ecosystem models when it comes to representing cephalopods ecology;
- Tackling the issue by improving the existing features of the Atlantis modelling framework and developing additional tools to represent the particularity of cephalopods ecology;
- Testing the sensitivity of the resulting model to various ecological processes and cephalopod life-history;
- Subjecting the model to an environmental change scenario and analysing the implications for cephalopods and other groups.

A preliminary investigation into the representation of cephalopod ecology in ecosystem models around the world asserts the limitations of our understanding of their impact on the system. I find that despite the frequent lack of data on cephalopod ecology, structural improvements to models could already bring valuable additional insights on their role in the ecosystem. I then focused on an ecosystem model of the South East of Australia region to investigate the role of cephalopods in the food web. New features were added to the Atlantis modelling framework and many mechanisms

disregarded until now were used to adequately represent the life-history traits of cephalopods; their exponential growth, their opportunistic and voracious feeding, their predation on relatively large prey; their ontogenic ecological shifts. The model was then subjected to a series of sensitivity tests to cephalopod parameters to identify the key ecological processes of this group and their impact on the structure and functioning of marine food web. This exercise revealed the potential of ecosystem models to adequately simulate cephalopod life-history traits, and pointed to the key importance of the growth capacity of squid species to drive their role in the ecosystem. The ecosystem model is also used to assess the impact of climate change on cephalopod ecology and on ecosystem functioning. An increase in temperature over 50 years, following one of the IPCC scenarios, is forced on the model. Results indicate that upcoming changes will benefit squid species as they take advantage of food-web changes better than many forage fishes that are both their competitors and their prey. The abundance of arrow squid, an oceanic squid, increases by about 15%, and the abundance of calamari, a neritic squid, increases by about 9% by the end of the climate change scenario. This leads to a substantial ecosystem change that could impact many species of interest for fisheries, and should therefore be taken in to consideration for the future of marine exploitation.

Acknowledgements

I would like to thank first my CSIRO (Commonwealth Scientific and Industrial research Organization) supervisor Beth Fulton, who made herself available to me all thorough the PhD. She was an exceptional teacher of the philosophy and functioning of the Atlantis tool and general ecosystem modelling, gave an unmeasurable help to upgrade the Atlantis code for my requests and needs, and still took the time to participate and improve the writing process. I also want to thank my main UTAS (University of Tasmania) supervisor Gretta Pecl, for all the time she took reviewing and improving all my writings, for her input on her much loved alien cephalopods, and her incredible help to deal with the administrative weight of the project. Both Beth and Gretta pushed me up the learning curve of PhD, and provided an incredible support thorough the personal experience and challenge this is. I would like to thank them particularly for the advice they gave me on the management of a career in research and ecology. Many thanks to my other UTAS supervisor Sean Tracey as well, who provided constructive and sharp comments on both the thesis and the university requirements. I also must and want to extend my thanks to Bec Gorton, whose technical help has been incredibly efficient up until the very end of my PhD, to fix any difficulty I faced using Atlantis and the IT tools associated. Her support and eagerness to help greatly helped to speed up the project and face the technical delays without too much stress. Thanks to the Atlantis team and to Gretta's students team, two teams who faced similar challenges as I while going through my PhD, and whose help and teamwork as always been a source of motivation. Particular thanks to Javier Porobic who was always keen to make me benefit from his own modelling and coding experience, and whose conversation on the world or Mr Wayne will be missed. Thanks to Derek Fulton as well, who kept the spirit of the office up with stories that will be missed as well. And finally, and most importantly, thanks to my family for being always supportive in complicated times and for pushing me to reach. Particular thanks to my parents who supported me during the last writing weeks of the PhD.

Table of contents

List of figures

List of tables

Chapter 1 General Introduction

Stories and legends of the Kraken, an ocean monster putting ships in peril, have aroused the imagination for ages, occasionally reinforced by the appearance of giant squids and other elusive deep-sea cephalopod species. Today, a new popular theme seems to be emerging: "the squid overlord". Although originated from fictional stories like *The Call of Cthulhu* of H.P. Lovercraft, its resonance in popular culture is probably associated with real events, like the expansion of the jumbo squid (Field et al. 2007) and their increasing abundance in catches (Doubleday et al. 2016).Their alien phenotype has been a curiosity among the animal domain, with three hearts (Schipp 1987), blue blood (vanBruggen 1980) and a neuronal network extending through their arms (Sander 1975). However, this exceptional phenotype is more than a simple curiosity, and is associated with ecological specificities, making cephalopods represent a unique component of ecosystems (Boyle & Boletzky, 1995).

Cephalopods have important feeding activity on a wide range of prey (Clarke, 1996; Coll et al, 2013; Rodhouse & Nigmatullin, 1996; Young et al., 2013), and are prey of many predators of ecosystems (Boyle & Rodhouse, 2005; Smale, 1996; Logan et al., 2013). They thus have a strong role in the transfer of nutrients up the food web in many areas (Cox et al., 2002; Griffiths et al., 2010; Olson and Watters, 2003; Rosas-Luis et al., 2003). Although our understanding is somewhat limited, cephalopods are thought to have an important role in food webs, and their abundance is growing worldwide, so improving our understanding of their role in ecosystems is becoming a major issue. This is even more so as cephalopods are relatively fast to respond to the effects of climate change and other environmental changes (Angilletta et al. 2002, Pecl & Jackson 2008). Moreover, cephalopod fisheries are quickly increasing worldwide, with little associated stock or ecosystem impact assessments (Anderson et al. 2011). The potential of these species to drive change in systems as they are submitted to pressures from environmental changes and fisheries thus needs to be investigated. I

need some insight on the processes regulating species impact on systems and their changes before non-reversible and potentially detrimental changes occur. It is an important step towards better understanding and management of marine resources at a time when human activities and systems are subjected to significant changes (Bracken et al. 2007).

The goals of this project are to assess the role of cephalopods in marine ecosystems and their potential influencing on the functioning of ecosystems linked to the responses of these species to environmental change. In the first chapter, I identify the limits of ecosystem models regarding cephalopod ecology, and assess the extent of this issue. I achieve this by building a framework to assess and compare the capacity of models to represent cephalopod species and identify at the areas of improvement. The second chapter is an attempt to address the issue by updating an Atlantis model of the South East Australia to better represent local cephalopod ecology. I try to bring new insights on their role in the system by testing the sensitivity of the model to different cephalopod species and the associated ecological processes. This allows us to identify the key ecological processes regulating the impact of species on the food web. The third chapter is turned towards the future, as I subject the model to different climate change scenarios. This last work allows us to point at the effect of environmental changes on cephalopod ecology and on ecosystem functioning. I analyse the relationship between climate-driven changes in cephalopod ecology and the resulting changes in ecosystems functioning and resources.

These chapters were written as distinct journal articles, and consequently there will be some overlap between them as a result, particularly in the introduction sections.

Cephalopods alien ecology and their importance in the food webs

Because of their voracious feeding activity, squid and other cephalopods exert a top-down control on their prey (Rodhouse & Nigmatullin 1996). Generally feeding on small crustaceans as juveniles, they

54 shift to micronekton, other cephalopods and larger fishes as they grow to maturity (Rodhouse &
55 Nigmatullin 1996; Parry 2006; Ruiz-Cooley et al. 2006). They can also act as top predators and may
56 feed on exploited fishes (Neira & Arancibia 2013; Field et al. 2007). Moreover, cephalopods can be
57 important prey of apical predators, such as large predatory fishes, seabirds and marine mammals
58 (Boyle & Rodhouse 2005; Logan et al. 2013; Smale 1996). Their swimming capability and use of
59 currents allows many species to migrate between distinct habitats (O'Dor 2002) while their dynamic
60 camouflage allows them to be efficient hunters (Adamo et al. 2006; Barbosa et al. 2008; Hanlon 2007;
61 Staudinger et al. 2011). All these factors give cephalopods an important role in energy and nutrient
62 transfer in food webs. They are often a key link between micronekton and many top predators (Cox et
63 al. 2002; Field et al. 2013; Griffiths et al. 2010; Olson & Watters 2003). In some systems,
64 cephalopods could play a keystone role, with the potential to significantly increase the speed of
65 nutrient transfer and to affect a large range of species in the ecosystem (Coll et al. 2013; Rocha et al.
66 2001; Smale 1996; Young et al. 2013).
67
68 However, despite occupying similar trophic levels as piscivorous fishes, cephalopod physiology sets
69 them apart and makes them a unique component of the ecosystems they inhabit (Boyle & Boletzky
70 1996; O'Dor & Webber 1986). They have a short lifespan of less than one or two years and often die
71 after spawning, although many species will spawn multiple times within one season (Van Heukelem
72 1976; Forsythe et al. 1994; Anderson & Rodhouse 2001; Pecl 2001; Rocha et al. 2001; Arkhipkin
73 2004). Cephalopods are also distinct from other species who share similar trophic levels (largely
74 teleosts) as they have a fast growth rate and metabolism that is supported by a voracious behaviour
75 (Rodhouse & Nigmatullin 1996; Rodhouse 2013; Semmens et al. 2004) and a high food conversion
76 efficiency (O'Dor & Wells 1987; Lee 1995). Cephalopods have an exponential growth curve and
77 reach maximum size just shortly before senescence (Moltschaniwskyj 2004). These traits provide
78 cephalopods with a potentially very important productivity (Nigmatullin, 2004; O'Dor & Wells,
79 1987), which has been observed to cause occasional high peaks of cephalopod biomass (Neira &
80 Arancibia, 2013; Rodhouse et al. 1998).
81

Cephalopods population dynamics and physiology are subjected to strong variability. Their recruitment can vary with great amplitude (Agnew et al. 2000), and the growth of individuals is highly variable and difficult to model (Jackson et al. 2003, Triantafillos 2002). The fast turn-over, high productivity and strong variability of cephalopod populations causes them to have a strong inter- and intra-annual variability compared to other components of the ecosystem (Bellido et al. 2001; Boyle & Boletzky 1996; Jackson et al. 1998; Rodhouse et al. 1998).

Despite this important role of cephalopods for food webs, our knowledge of their ecology is still incomplete (Roper & Shea, 2013, Lindgren et al., 2004). Their highly variable dynamics, their elusiveness and complex behaviour makes them difficult to study (Allock et al. 2017). To this day, there is no reliable method to predict future recruitments (Pierce & Guerra, 1994; Rosenberg et al. 1990). While a significant body of literature is available on the diet of cephalopods, the studies remain subject to strong biases and uncertainty. Studies of stomach content tend to have a low robustness due to the ingestion mode of cephalopods, who chop pieces of flesh off their prey (Ibañez et al. 2008). Isotope studies are too scarce to be used regularly in cross-examination with gut content despite their contribution to trophic studies. In a similar way, the importance of cephalopods in top predators' diet also suffers large uncertainty and is difficult to estimate as their flesh is generally digested faster than fish flesh. While their hard parts (e.g. beaks) are largely undigested and can be a longer term record of consumption they can survive consumption of their primary predator by a secondary predator, creating prey-of-prey confusion (Santos et al. 2001).

Insights and lessons from ecosystem models

In this study, I consider an ecosystem as a set of processes directing the flow of matter and energy between the environment and local organisms within a given area (Blew 1996). Considering the interactions between all these elements has become a recognized necessity and the ecosystem approach has been an increased focus lately (Beaumont et al. 2007, Loreau et al. 2001, Sherman et al.

2005). In this perspective, the use of ecosystem models has been increasing over the last three decades in order to use information from relatively focused studies (i.e. on single species, single life stage or single processes) in a broader frame. These models typically aim to represent the processes involved in ecosystem functioning, covering physical, chemical and biological phenomenon (Fulton 2010). They are powerful tools for grasping a broad understanding of ecosystem structures and the indirect impacts of various components on one another. They bring new insights on ecosystem functioning, clarifying various species' role, identifying key species (Libralato et al. 2006, Stevens et al. 2000) and nutrient pathways through the food web (Friedland et al. 2012).

However, these models often fail to represent cephalopod ecology with robustness (Coll et al. 2013; Bulman et al. 2011; Guénette 2013). They lack adequate processes to represent the particularities of cephalopod ecology and suffer from the recurrent lack of information or certainty on their life-history trait parameters. As a result, little that is conclusive can be drawn from most of the current models when it comes to cephalopod impacts on marine systems. Assessing the capacity of models to represent species ecology is not an easy task. The first consideration is the quality and robustness of the data used to parameterize functional groups. This is a relatively simple method and it is an option already available in some modelling frameworks (Christensen & Walters 2004), but this information is seldom displayed in articles and rarely discussed. To go further than simply data assessment, considering the adequacy of actual processes represented would provide more information on models capacities. However, few studies detail the actual adequacy of processes implemented in the model to represent the dynamics of species of particular ecology like cephalopods. The sensitivity analysis on ecosystem models can then point at the areas which lack robustness and may temper our capacities to represent the functioning of ecosystems and the interactions between the ecology of various species. These types of investigation can allow us to identify needs for improvement in models structure and point at particular processes that require more research if we are to understand the mechanisms driving marine systems.

Confronting our understanding of cephalopod ecology and its influence on food web and ecosystem dynamics could give us insights on missing information. The response of models to the representation of cephalopods could allow us to identify the key processes regulating their role in the system and could point at eventual lack of robustness in our knowledge (Fennel et al. 2001). The assessment of system sensitivity to groups with such variable and quickly evolving ecology is a major challenge for today's marine sciences. It is a necessary step towards a better appreciation of future changes in ecosystem functioning

Climate change and human activities are currently putting ecosystems under heavy pressure, driving them towards conditions unseen for millions of years, possibly with irreversible transformations (Doney et al. 2012, Hoegh-Guldberg & Bruno 2010). Species changes in distribution, or range shifts, of various species, including cephalopods, are already expected to modify ecosystem functioning (Marzloff et al. 2016, Ramos et al. 2015). The improvement of the representation of ecological mechanisms is an important step towards predicting future changes of systems. Modelling studies based on purely empirical and statistical evidences seem to show limits. If the performance of a model to depict past observations is a mark of relevance, it is not a very robust proof of its performance to describe systems changes in entirely new conditions. Identifying key mechanisms driving the response of ecosystems and their future changes is thus a key step if we want to identify any shifts in systems functioning.

The evaluation of ecosystem model performances is often based on their capacity to hindcast (i.e. replicate trends observed in past observation. However, the value of this test strongly depends on the informative value of the observations i.e. the test is informative only if 1/ past data is contrasted due to the effects of various mechanisms, or 2/ there is the mark of a mechanism in the observations, or 3/ there were ecological changes in the past and they are reflected in observations. The capacity of a model to represent future change can be thus put in doubt. For these reasons, the statistical performances of models should not be the only goal, as a deep understanding of the mechanisms driving ecosystems responses to changes is key to obtain an insight on unprecedented changes. The

implementation of the effects of environmental changes on ecosystem processes is thus a major challenge to foresee future changes.

Potential role of cephalopod species as drivers of ecosystems' functioning and services

Shifts in ecosystems' food webs are driven by some key species (Piraino et al. 2002; Tilman 2000). Cephalopods are at the centre of food webs with an important role in the transfer of nutrients, and could thus become an important regulator of marine ecosystem functioning. Cephalopod species are very sensitive to external changes. As ectotherms, they are particularly sensitive to temperature changes (Angilletta et al. 2002), and the effects of salinity and ecology on their ecology have already been observed (Bazzino et al. 2005, Payne et al. 2011, Seibel 2007). The important variability of cephalopods ecology, their sensitivity to their environment and their fast turn-over gives them a potential advantage to respond and adapt to environmental changes faster than other species (Berteaux et al. 2004). The resulting capacity to fill vacant ecological niches (Caddy & Rodhouse 1998, Pecl & Jackson 2008) is probably one of the reasons behind their global increase in abundance worldwide (Doubleday et al. 2016). Our understanding of future ecosystem changes would thus be significantly improved by addressing the uncertainties around the impact of cephalopods on the system. It is important to understand the mechanisms driving various species reactions to external changes and how they will interact with each other to identify the future dynamics of marine systems.

This type of research also provides an extremely valuable insight for the management of marine resource exploitation as catches of cephalopods are increasing worldwide due to their increase in abundance and a renewed interest from fisheries (FAO 2015). In Australia, catches of cephalopods by fisheries have increased substantially from the end of the 1970s, rising from a couple hundred tonnes in the 1975 to 2000-7000 tonnes since 2000 (FAO 2016). Although two squid species, *Nototodarus gouldi* and *Sepioteuthis australis* comprise the major part of catches, fisheries capture a variety of species including octopi – such as *Octopus pallidus* and *Octopus tetricus*, – and cuttlefishes (e.g.

191 *Sepia apama*; Nottage et al. 2007). In the last four decades, the economic and provisioning role of
192 cephalopods for fisheries worldwide has continued to grow, with annual harvest now more than 4
193 million tonnes (in 2013), representing 5% of the total harvest of all species from marine waters
194 (Caddy & Rodhouse 1998; Hunsicker et al. 2010, FAO 2015). However, the importance of
195 cephalopods for fisheries cannot be estimated only by their catches. As key prey sources, on average
196 cephalopods support approximately 15% of marine fisheries landings by weight and 20% by landed
197 value (Hunsicker et al. 2010). This highlights their role in the support of ecosystem services, and the
198 need to assess management of cephalopod fisheries with an ecosystem approach if we want to ensure
199 the sustainability of ecosystem services.
200

201 **Interests of South East Australian region and local ecosystem model**
202

203 The use of ecosystem models to gather and confront our knowledge of cephalopod and other species
204 ecology can bring valuable insight. However, the more information available there is on their ecology,
205 the more robust are the conclusions of the models. In this regard, a significant body of work has been
206 done in South East Australia (Green 2011, Stark 2008, Steer et al. 2007, Triantafillos 2002). This is
207 also a rapidly warming region of "hotspot" (Hobday & Pecl 2014) and thus provides an exceptional
208 opportunity to gain insights on transformations that will occur later over the globe (Pecl et al. 2014).
209 These two criteria highlighted the region as a great area of focus to study the changing nature of
210 cephalopods' role in ecosystem functioning.
211

212 To understand better the challenges that are to come, I am updating a South Eastern Australian model
213 to more effectively represent the role of cephalopods and to evaluate their impact on marine
214 ecosystems. Among the several model of the region (Bulman 2006, Fulton & Johnson 2012,
215 Goldsworthy et al. 2013), I chose the models from Johnson (2013) covering a relatively wide area and
216 encompassing both the neritic and oceanic habitats in order to avoid emphasizing one part of the food
217 web. The updates are primarily focused on cephalopod species or closely linked functional groups

(i.e. direct predators). The effect of climate change following different IPCC scenarios on the oceanography of our model has already been implemented, and thus was already available for us to introduce to our ecosystem model. The implementation of various climate change scenarios and fishery management strategies should allow us to assess the changing nature of cephalopod ecology and ecosystem functioning, and give an insight to the consequences on fisheries resources. This points to the outcomes of various management strategies and could allow us to identify opportunities and risks associated with climate change in terms of biodiversity, ecosystem functioning and ecosystem services. This work could give us a strong insight into the future changes that are emerging worldwide due to climate change and human exploitation. It could also ultimately provide valuable insight to improve Ecosystem Based Management to better adapt the exploitation of marine resources to climate change, whether it is to mitigate human impact on systems or/and to optimize marine resources use.

Chapter 2 The ecological role of cephalopods and their representation in ecosystem models.

Abstract

Cephalopods, especially squids, are believed to have a structuring role in marine ecosystems as a link between different trophic levels, primarily due to their voracious prey consumption and high production rate. Cephalopod ecology, however, is still poorly understood as observational studies often give highly uncertain and variable results due to the peculiarities of cephalopod behaviour and biology, and their responsiveness to external drivers. This review evaluates our representation of cephalopods in ecosystem models and the insights given by these models on the role of cephalopods in our oceans. We examined ecosystem models from 13 regions to analyse the representation of cephalopods and compared their results to local trophic studies. Our analysis indicated that most ecosystem models inadequately include cephalopods in terms of model structure and parameterization; although some models still have the capacity to draw valuable conclusions regarding the impact and role of cephalopods within the system. Oceanic squid species have a major role linking trophic levels and food webs from different habitats. The importance of neritic species varies locally, but generally cephalopods have a substantial impact via their consumer role. To better understand the ecological role of cephalopods, improved representation of these species in ecosystem models is a critical requirement and could be achieved relatively easily to more accurately articulate the mechanisms regulating the ecological role of cephalopods.

Introduction

The importance of squids to society goes beyond the legends and mythologies of ocean monsters with giant tentacles. In the last four decades, the economic and provisioning role of cephalopods for fisheries has continued to grow, with annual harvest now more than 4 million tonnes (in 2013), representing 5% of the total harvest of all species from marine waters (Arkhipkin et al. 2015; Caddy & Rodhouse 1998; Hunsicker et al. 2010, FAO 2015). However, the importance of cephalopods for fisheries cannot be estimated only by their catches. As key prey sources, on average cephalopods support approximately 15% of marine fisheries landings by weight and 20% by landed value (Hunsicker et al. 2010). In some areas, this indirect contribution of cephalopods can reach up to 55% of the landings (tonnes) and 70% of the value of fisheries. Approximately 75% of this contribution is made by providing a food resource to exploited species like finfishes that are feeding on them (Hunsicker et al. 2010). Thus, consideration of the ecological roles of cephalopods is necessary for developing a more complete understanding of ecosystem dynamics and of the true importance of cephalopods to ecosystems and the human societies dependent on them, although knowledge of their ecology is still incomplete (Lindgren et al. 2004; Roper & Shea 2013). This chapter aims to identify the caveats of ecosystem models attempting to represent cephalopods and propose a way forward for addressing these limits and improving our understanding of the ecological role of cephalopods.

Because of their voracious feeding activity, squid and other cephalopods are believed to exert a top-down control on their prey (Rodhouse & Nigmatullin 1996). Generally feeding on small crustaceans as juveniles, they shift to micronekton, other cephalopods (including cannibalism) and larger fishes as they grow to maturity (Rodhouse & Nigmatullin 1996; Parry 2006; Ruiz-Cooley et al. 2006). Due to their exceptional capture apparatus (i.e. prehensile arms and tentacles) they have the capacity to grab or even bite flesh off relatively large animals and thus prey on a wide size spectrum (Rodhouse & Nigmatullin 1996). They can thus act as top predators and may feed on exploited fishes (Neira & Arancibia 2013; Field et al. 2007). Moreover, cephalopods can be important prey of apical predators, such as large predatory fishes, seabirds and marine mammals (Boyle & Rodhouse 2005; Logan et al.

2013; Smale 1996). Their swimming capability and use of currents allows many species to migrate between distinct habitats (Ibáñez et al. 2015; O'Dor 2002) while their dynamic camouflage allows them to be efficient hunters (Adamo et al. 2006; Barbosa et al. 2008; Hanlon 2007; Staudinger et al. 2011). All these factors give cephalopods an important role in energy and nutrient transfer in food webs. They are often a key link between micronekton and many top predators (Field et al. 2013; Griffiths et al. 2010; Olson & Watters 2003). In some systems, cephalopods could play a keystone role, with potential to significantly increase the speed of nutrient transfer and affect a large range of species in the ecosystem (Coll et al. 2013; Rocha et al. 2001; Smale 1996; Young et al. 2013).

Cephalopods have a peculiar ecology and are a unique component of the ecosystems they inhabit (Boyle & Boletzky 1996). They have a short lifespan of less than one or two years and often die after spawning, although many species will spawn multiple times within one season (Van Heukelem 1976; Forsythe et al. 1994; Anderson & Rodhouse 2001; Pecl 2001; Rocha et al. 2001; Arkhipkin 2004). This leads to cephalopod populations having strong inter- and intra-annual variability compared to other components of the ecosystem (Boyle & Boletzky 1996; Rodhouse et al. 1998). Cephalopods are also distinct from other species that share similar trophic levels (e.g. largely teleosts) as they have a fast growth rate and metabolism that are supported by a voracious predatory behaviour (Rodhouse et al. 1998; Rodhouse & Nigmatullin 1996) coupled with a high food conversion efficiency (O'Dor & Webber 1986; Lee 1995). These traits result in cephalopods having potentially high productivity (O'Dor & Webber 1986; Nigmatullin 2004) which can lead to occasional strong peaks in cephalopod biomass (Rodhouse et al. 1998; Neira & Arancibia 2013).

The high turn-over rate of cephalopod species, as a function of their short life-spans, and their sensitivity to environmental changes, are likely to give them the opportunity to respond faster than many other species to climate change and to fishery pressures (André et al. 2010; Berteaux et al. 2004; Caddy & Rodhouse 1998; Hughes et al. 2005; Pecl & Jackson 2008). This responsiveness could increase the importance of their role in ecosystem function and their provisioning role for global fisheries in the future. However, there are still strong uncertainties regarding both the ecology and the

abundance estimates of these species (Cherel et al. 2008; Field et al. 2007; Lee 1995; Piatkowski 2001; Pierce & Guerra 1994; Wormuth & Roper 1983). More information on the causes of population variability and on the interactions of cephalopods with other species would significantly improve our understanding of ecosystem functioning.

The particularities of cephalopod ecology and their role in ecosystems led to the organization of many conferences with a specific focus on cephalopods, including those hosted by the Cephalopod International Advisory Council (CIAC) (Jackson et al. 2007) or the ICES (Piatkowski 2001) and many other workshops (Moltschaniwskyj et al. 2006). A great deal of new research on ecosystem functioning and cephalopod ecology has been produced over recent years, bringing new knowledge of the role of these species in ecosystems. Synthesising this information into a coherent broader understanding and identifying knowledge gaps pertaining to the roles of cephalopods in food webs can provide knowledge to facilitate better management of exploitation of marine ecosystems and food resources (Anderson et al. 2011), and more robustly predict how this important group may respond to climate change. This is a large task and not necessarily tractable in a single study. As a first step to address this issue, here we assess the current representation of cephalopods in ecosystem models and suggests the necessary improvements that could be undertaken to enhance our understanding of their ecological role. We have chosen to restrict our work to ecosystems where there is interaction between the open ocean and the shelf, as these regions of high productivity typically host a wide variety of cephalopod species.

Cephalopod species are concentrated in coastal areas and adjacent open waters (Roper et al. 2005; Tittensor et al. 2010; Voss 1967), and so our study focuses in these areas. In many coastal areas, the inputs and recycling processes of nutrients, and associated enhanced primary productivity, means these regions host a high species richness (Longhurst et al. 1995; Roper et al. 2005; Thomas & Borges 2012). Moreover, the warmer temperatures of coastal waters support greater activity at a lower metabolic cost (Clarke & Gaston 2006; Currie et al. 2004; Tittensor et al. 2010) and the waters are nutrient (and prey) rich due to the input of terrigenous nutrients and upwelling of deep-ocean water up

the slope and onto the shelf (Seitzinger & Giblin 1996). The episodic nature of upwelling events and river flows can make the environment highly variable, more than doubling productivity in short pulses (Yoder et al. 1983; Eadie et al. 1994), meaning species like some cephalopods that can respond quickly see maximum benefit. The productivity of shelf waters has a broader footprint, however, as excess production and nutrients (rapidly remineralised in shelf sediments) are exported to adjacent coastal sea waters (Thomas & Borges 2012). The export of carbon is enhanced by strong benthopelagic coupling, facilitated by the close proximity of these habitats in shallow waters.

In general, cuttlefishes are primarily demersal species occupying continental shelf areas in warm and temperate waters. Octopus species live in benthic habitats and range from shallow coastal waters down to approximately 5,000m (Collins et al. 2001; González & Sánchez 2002). Octopuses and cuttlefishes generally dominate demersal assemblages of neritic areas (Quetglas et al. 2000; Boyle & Rodhouse 2005; González & Sánchez 2002). In contrast, squid species dominate the water column (Quetglas et al. 2000; Boyle & Rodhouse 2005; Brunetti et al. 1998). Except for some shallow water species and reef species (Boyle & Rodhouse 2005), most squid species inhabit pelagic habitats. For example, Loliginids are distributed in neritic areas; Gonatids are present in oceanic waters adjacent to the continental shelf; and the Ommastrephid family, which represents more than half of the world's cephalopod fishery catch, undergo seasonal migrations between oceanic and shelf waters (Boyle & Rodhouse 2005; Roper et al. 2005). The jumbo squid for example, an iconic species of Ommastrephid, is mostly exploited by inshore fisheries, but also sustains an important offshore fishery off the south American coast (Rocha & Vega 2003). The migrations undertaken by many of these oceanic species are an important link between food webs of the open ocean and neritic waters (Roper et al. 2005; Brunetti et al. 1998; Arkhipkin 2013). It was thus important that the work reviewed here covered both neritic and adjacent oceanic habitat.

Globally, cephalopod species are recognized as a major component of many marine ecosystems. They are present in all marine waters with a distribution from the surface layers down to several thousand meters; on the continental shelf and in the open ocean; from the poles to the equator. Coastal and shelf

areas have high primary and secondary productivity (Longhurst et al. 1995), host a wide variety of squid, octopod and cuttlefish species (Clarke 1996; Haimovici & Perez 1991; Quetglas et al. 2000), and are likely to be particularly strongly influenced by cephalopod species. Additionally, these regions also concentrate human impacts by hosting intensive marine fisheries, aquaculture, tourism and resource extraction activities (Halpern et al. 2008); understanding the functioning of these ecosystems will underpin and facilitate ecosystem-based and sustainable management.

Dynamic ecosystem models have been used by Coll et al. (2013) (Coll et al. 2013) to support a broad literature review of the importance of squids in ecosystems around the world. However, this valuable study focused on an impact index, and it was not within its scope to discuss the differences in roles and modalities of impact of various groups of cephalopods or the issue of missing information and its implications for model parameterisation and results. Considering that many studies point at the issue of the representation of cephalopods in models and the uncertainty of their parameters (Coll et al. 2013; Gasalla & Rossi-Wongtschowski 2004; Bulman et al. 2011; Guénette 2013), our goal is to evaluate the adequacy of ecosystem models to assess the role of these groups in marine systems, and the potential effect on our understanding of ecosystem functioning. To achieve that, we first evaluate the representation of cephalopods in models, the quality of data associated with their parameterization and the structure of the model. We then assess the sensitivity of models by analysing their results and quantification of the impact of cephalopods. We identify cephalopod traits associated with the role of different functional groups and their impact on the system. We also compared these results with more common studies using alternative approaches to examine the trophic ecology of cephalopods in our areas of interest to determine if the outputs of the models we examined were consistent with previous understanding of the ecological role and impact of cephalopods. We then highlight the improvements that can be made to better understand the ecological role of cephalopods and identify ways in which our understanding of the ecological processes involved can be advanced.

Methods

To analyse the adequacy of models to assess the role of cephalopods, we considered two main elements. The first is the quality of data used in the parameterization, as it will affect models conclusions and their robustness. The second is the structure and processes representing cephalopod ecology in the model, which will influence the potential insights and results of models. We ranked these two criteria for each model to combine them and evaluate the adequacy of models and of the insights they can give. The role of cephalopods in ecosystem models is obtained from indexes that are measures of a group's impact on the system. We then compare the results from these models with findings from other approaches, gathered from studies that provided direct insight on the trophic role of cephalopods.

We reviewed a wide range of studies used to estimate cephalopod parameters in models, and allocated different scores as indexes of the data robustness (appendix 2-1). The types of data and studies used to provide this information include fisheries catches and trawl surveys (Chambers & Dick 2007; Rodhouse et al. 1995; Rodhouse et al. 2014; Watanabe et al. 2006) to indicate the abundance, distribution and habitats of cephalopod species. Diet composition, isotopic and elemental analysis of cephalopod species and their predators (Parry 2006; Takai et al. 2000; Clarke 2006; Cherel et al. 2009) also give indices of their distribution, and show their trophic links and interactions with other species. A key determinant of the role of cephalopods as system connectivity agents is their movement and migration patterns. This has largely been explored using tagging studies, either physical (e.g. electronic) tags (Pecl et al. 2006) or chemical tags (Pecl et al. 2010; Semmens et al. 2007). Cephalopod growth and production has been studied through laboratory growth studies (Forsythe et al. 1994), and analysis of statolith increments (Quetglas & Morales-Nin 2004) or beak increments (Perales-Raya et al. 2010) from wild-caught animals.

To rank the quality of data, we allocated scores based on the type of data used and its origin, whether it is sourced from ecological studies, expert knowledge or informed opinion, or estimated as required

to balance the model. Due to the inherent complexity of ecosystem models, we focused our analysis on some key parameters (table 2-1) and used the mean score of parameters for each model. If a model displayed several cephalopod groups, we only considered the group with the best score. We thus avoided giving a lower score to models with a good representation of a key cephalopod species with relatively strong impact on the system and a less robust representation of species of minimum importance.

Table 2-1. parameters considered in scoring the quality of data of the model. for each of those parameters, we looked into the source of information used to build the model and assigned a corresponding confidence score.

EwE	**Atlantis**
Biomass	Biomass
Consumption	Search volume
Predators diet (production)	Predators diet
Diet	Diet
Distribution and movement	Distribution and movement
—	Predators size selectivity
—	Habitat protection
—	Growth
—	Recruitment

Parameters involved in similar processes between models are aligned, although it should be noted that equivalences are rarely complete. We excluded vulnerability and prey preferences parameters (respectively from EwE and Atlantis) from the study. These parameters are known to be highly uncertain (as they are not directly measurable) and are estimated through the calibration process, fitting the model to observations, after other parameters (across the entire food web) are estimated. Consequently, including them would bring all score down across the board and would not assist the comparisons.

In Ecopath with Ecosim (EwE) (Christensen & Walters 2004), a relatively commonly used ecosystem modelling framework, the 'Pedigree index' allows assignment of a score to each parameter based on the origin of the data used to build the model. However, this index was too seldom given in model reports and papers using EwE for it to be used here. We thus built a less detailed but relevant quality

ranking framework which allowed us to assign a score ourselves and to also consider a broader range of ecosystem models (e.g. Atlantis) rather than only EwE models (table 2-1 and 2-2). This marking method was applied to both EwE and Atlantis studies. Only these two types of models were included because they are the most commonly found at present. OSMOSE models (Marzloff et al. 2009) have resolved squid in a way that resolves some of the issues identified here, but still essentially treats them like fish. Consequently, by restricting our review to the most common modelling platforms we can provide lessons for new implementations of those models and to the development of other modelling platforms.

Even though we have decided not to score these parameters involved in diet determination, it is worth noting that there is a documented lack of precision in cephalopod diet studies (Field et al. 2007; Ibáñez et al. 2008; Rodhouse & Nigmatullin 1996) and in their estimation in predator diets (Staudinger et al. 2013). The strong variability in growth (Chen & Chiu 2003; Jackson et al. 2003), recruitment (Berteaux et al. 2004) or behaviour (Staudinger et al. 2011) and difficulty in identifying the processes controlling these, has led to relatively poor inclusion of cephalopods in ecosystem models (Fulton 2010). We therefore thought it necessary to clearly separate the last two categories of data quality (table 2-1) due to this important bias of many cephalopod studies.

The ranking of model structure is based on the representation of cephalopod functional groups and the associated ecological processes. A different grouping or representation of processes would allow for different trajectories and for different conclusions to be drawn regarding the species concerned. Models with distinct functional groups for cephalopod species and with more detailed processes are thus given higher scores, while models representing all cephalopods in a single groups with limited details receive lower scores.

464 **Table 2-2. Scoring framework to evaluate the adequacy of ecosystem models to assess the role of**

465 **cephalopods.**

Data quality evaluation		
Score	Parameter origin	Description and examples
1	Model results	Estimation from other models or based on the model equations.
2	Rough estimates	Estimations based on occasional observations, empirical relationships or assumptions particular to the group or species.
3	Local sampling low precision	Sampling not necessarily focused on the group of interest or may be subject to important bias or limits of sampling. i.e. diet based on stomach content studies biased by the ingestion and digestion process of predators i.e. biomass estimate based on fisheries-dependent data.
4	Local sampling high precision	Sampling from the area of interest focused on the group of interest. i.e. diet information using both stomach and isotopic studies. i.e. biomass based on fisheries data backed up with independent scientific surveys.
Structural implementation evaluation		
Score	Cephalopod groups structure	Description and example
1	One mixed group for all cephalopods	One single group representing all cephalopod species or only the main ones.
2	Aggregated groups of biomass pools.	Generally aggregation of squid species or pelagic species while octopods or benthic species are in other benthic groups.
3	Stage structured biomass pools	Key species are represented by their own groups with stage structure (juveniles and adults).
4	Aged structured detailed cephalopod	Species represented in various groups, with a growth model, eventual spawning event/s and recruitment assessment

Overall adequacy of models to represent cephalopod ecology – final score designation

		Structural Implementation			
		1	2	3	4
data quality	1	I	II	II	II
	2	II	III	III	III
	3	II	III	IV	IV
	4	II	III	IV	V

Comments on the evaluation of model adequacy and the potential conclusions on the role of cephalopods

I	Poor data and structure, no conclusions possible on cephalopods. (Both scores are 1)
II	Poor data or poor structure resulting in inadequate representation of the role and processes of cephalopods; no conclusions possible. (One score is 1, the other one is 1 or higher)
III	Balanced minimum detail in data or structure: conclusions could provide valuable insight but are limited or lack precision and should be confirmed via other sources. (One score is 2, the other one is 2 or higher)
IV	Good structure and data, models relatively robust with appropriate conclusions on the impact of cephalopods, although the processes regulating their role are not clear. (One score is 3, the other one is 3 or 4)
V	Structure and data well-adapted for cephalopods, strong conclusions on the role of cephalopods and the processes regulating it. (Both score are 4)

Categories represent the type of data and model structure used to represent cephalopods, and are allocated a score. The data quality evaluation is based on the relative robustness of cephalopod parameters derived from various sources of information. The structural implementation adequacy is based on the coherence of the functional grouping of cephalopods and the processes represented. Distinct functional groupings with detailed representation of processes are given a higher score. 1=lowest implementation or data quality, 4=highest. These scores are then combined to determine the overall model adequacy to assess the ecological role of cephalopods in each ecosystem. The lowest score of the structure implementation or data quality was considered the limiting factor in a given model. We thus used the lowest score to arrive at the final overall score of the implementation. All models-scores are outlined in appendix 2-2. For example: for the model of Tasmanian waters presented in Watson et al. (2013); average data quality score is 1.7 (rounded to category 2); and structure quality is scored as 3; its overall adequacy for representing cephalopod ecology is thus 3.

An overall model quality score, combining the two previously mentioned component scores, allowed us to evaluate the adequacy of models to assess the role of cephalopods and their likely impact on the ecosystem (table 2-1). Models with high data quality are not very informative if the biological mechanisms are poorly represented. On the other hand, a model with very detailed processes but low quality data would lack robustness and be purely speculative. The overall score of models is thus based on the lowest mark between the structural appropriateness and data quality. However, the model quality score refers only to the adequacy of the way cephalopods are included in the model and we recognise that this was not the explicit focus of many of the models. Models maybe for example focused on entirely different species or processes and provide very good conclusions in that regard, but have a poor capacity to assess the potential role and impact of cephalopods.

To assess the role of cephalopods in the system we used the keystoneness index and relative contribution to the biomass flow through the overall model to give an indication of the impact of a group on the system relative to the group's biomass. A keystone group is a group that would significantly affect other groups even with a relatively small change in biomass (Libralato et al. 2006). The biomass flow in a system is the amount of nutrient that is transferred between the various groups.

494 The relative contribution to a system's total biomass flow is an indicator of the importance of a group
495 in the transfer of nutrient from lower trophic levels to top predators.

496 **Table 2-3. Assessment of the relative impact of cephalopods on the ecosystem considered within**
497 **each model.**

	General description	Keystoneness index	Relative contribution to flow index
1	Small role: small impact on direct predators and prey	Lower than -1.5	Fourth quarter of groups with lowest contribution
2	Localised or limited role: strong impact on some direct predators and prey	Between -1.5 and -0.5	Second and third quarter
3	Secondary role: strong impact on several groups including indirect trophic controls	Between -0.5 and -0.25	First quarter excepting the top three contributors
4	Key role: strong impact on a large part of the food web	>-0.25	The three groups with highest contribution

498 The keystoneness index and relative contribution to flow were obtained from results of EwE models available
499 on EcoBase (http://sirs.agrocampus-ouest.fr/EcoBase/). A high keystoneness index is close to 0 while groups
500 with smaller impact have lower (more negative) keystoneness. The relative contribution to flow is an estimate of
501 the part of nutrient flow in the system that go through groups.
502
503
504 In order to identify new insights from ecosystem models, we compared model results with insights
505 from other approaches, gathered from studies that provided direct insight on the trophic role of
506 cephalopods (appendix 2-3). While predator diets provide direct information on the role of
507 cephalopods as prey and their potential bottom-up impact, cephalopod diet and consumption
508 estimation studies provide a direct indication of their top-down impact. Some of these studies were
509 used to implement models, and are therefore reflected in scores. However, additional or posterior
510 work allowed us to confront the outputs of models with results from ecological observations from the
511 field.
512
513 Lastly, we recognise that our scoring scheme is somewhat subjective and was completed by
514 researchers not directly involved in actual model construction. In order to test the robustness of our
515 review and validate the scoring, we contacted modelling experts that had developed one or more of

the models reviewed from each region (appendix 2-5). We requested that they assign scores to their own models following our framework, assessing the quality of data they used and the impact of cephalopods in their model. We received feedback from five of our areas of interest, providing a first estimate of the validity of the method.

Results

While limited in terms of the number of responses received, the feedback received from the model experts suggests that our scoring of the model implementation is accurate. Our scores of the impact of cephalopods on the system could, however, be less reliable in areas where there is also a low implementation score, as they are not believed to have a key role in the system. Nevertheless the scoring is seems a useful approach for understanding the efficacy of modelling approaches.

Adequacy of ecosystem models to assess the ecological role of cephalopods

Many of the models considered (20 out of 51) had a final implementation score of 1 or 2, and thus were assessed as inadequate to focus on the role of cephalopods in ecosystems and the processes involved (table 2-4). Some models do have the capacity to give a valuable insight of the impact of cephalopods (29 out of 51), but the structure of the model limits the conclusions of many of them. Only two models were considered adequate to provide good insights on this topic. We could not find any models with both structure and data adapted to adequately consider cephalopod ecology.

Table 2-4. Adequacy of the implementation of cephalopods in ecosystem models.

		Structural implementation			
		1	2	3	4
data quality	1	3	4	0	0
	2	10	10	1	0
	3	3	18	2	0
	4	0	0	0	0

536 Colours represent the global model adequacy to assess role of cephalopods, following the colour code displayed
537 in table 2-3. Numbers inside the table correspond to the number of models that we allocated to that category.
538
539

540 The lack of data is a common issue across models (table 2-3), with only 23 models being built with
541 local data. We could not find a model with most parameters built with good information based on
542 local studies of high precision. Gut contents of cephalopods and fisheries catch data were regularly
543 used to estimate predator-prey behaviour and biomasses, with little information available to address
544 the biases and limits of these studies.
545
546 However, the poor inclusion of cephalopods in ecosystem models is the primary concern, with only
547 three models with specific groups for key species. We found 16 models with only one single group for
548 all cephalopods combined and 32 models with only one clear group representing some cephalopod
549 species while others were part of more generalist groups. An improvement in the way cephalopods are
550 included in these models would clearly substantially improve the adequacy of models (table 2-3), and
551 many of the existing models could provide more robust and meaningful results on this important
552 component of the ecosystem.

553 **Ecosystem models and cephalopods' impact on the food web**

554 We could score the role of cephalopods in 23 models out of the 59 considered. Models with better
555 implementation often show a higher impact of cephalopods; although this is not universal, with some
556 of them still showing a secondary impact of these species on the food web (Link et al. 2010; Lassalle
557 et al. 2011). These results indicate that the quality of cephalopod implementation in a given model is
558 not correlated with the impact of cephalopods found in that model. Improving the representation of
559 cephalopods in models would therefore not result in a bias (artificial enhancement) regarding their
560 perceived importance. On the contrary, model improvements would likely allow for substantial
561 advancement in the reliability and robustness of the results of ecosystem models. This is even more so

for models showing a potential strong impact of cephalopods in the system, but where their implementation is too poor to draw conclusions regarding their role.

Table 2-5. Evaluation of the implementation and role of cephalopods in ecosystem models.

		Impact score			
		1 (low)	2 (limited)	3 (substantial)	4 (high)
Model adequacy	1 (inadequate)				1
	2 (minimal)	4	3	2	2
	3 (average)		2	3	6
	4 (good)				

Note only the 23 models in which we could allocate an impact score are displayed in this table.

We observed no key difference between implementation quality in EwE compared with Atlantis models even though Atlantis parameterization can be more demanding (appendix 2-2). This seemed to be due to the grouping of ecologically different species and relatively poor estimates of parameters in both frameworks.

In six geographical areas out of 13, the implementation of cephalopods is insufficient, given their suggested impact on the system, and improvements to the model could bring new understandings of the ecosystem functioning (fig 2-1). In three areas, models are adequate enough to provide valuable insight on the role of cephalopods, but improvements in their representation in the models could bring even greater understanding of their role, and importantly, the processes involved.

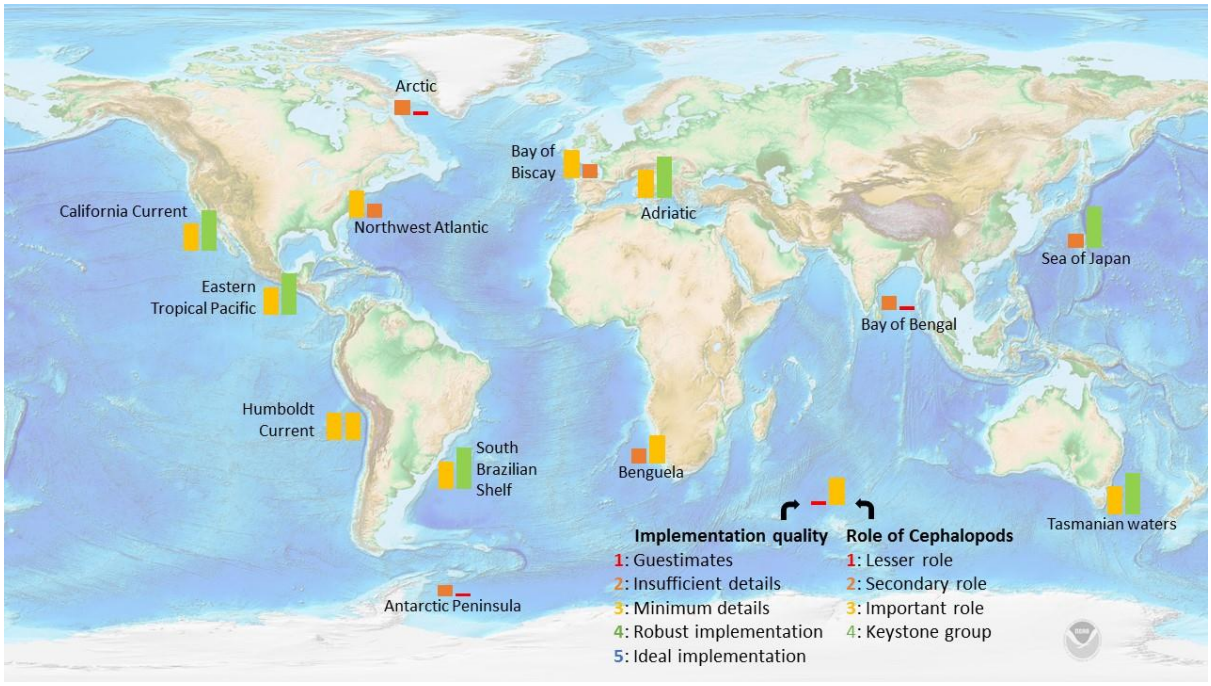


Figure 2-1. Role of cephalopods in ecosystem models around the world.

Results were taken from the best implemented model in the area presenting an indicator of cephalopods impact (appendix 2-2 and 2-4). We only display the impact score of the highest impacting cephalopod group. The quality of the implementation generally depends on the number of studies and information available locally, or on the degree of focus of local modelling studies on cephalopods. A robust conclusion on the role of cephalopods can be drawn when the "implementation score" is higher than the "role score". When the "implementation score" is lower than the "role score", uncertainties in cephalopod parameters and implementation may mean there is high uncertainty regarding the impacts. When the scores are even, there is some uncertainties but strong insights could still be drawn.

In six geographical areas (California Current, Eastern Tropical pacific, South Brazilian Shelf, Adriatic, Sea of Japan and Tasmanian waters), cephalopods appear to have a strong impact on a large part of the food web (fig 2-1). In two areas (Humboldt Current and Benguela current), they have a strong impact on direct and indirect trophic links, and in a further four areas (Northwest Atlantic, Arctic, Bay of Biscay and Bay of Bengal), they have a secondary or lesser role with only a relatively small impact on some prey and predators. The key role of oceanic cephalopods as a link between oceanic top predators and neritic food webs has been highlighted both in ecosystem models (Arancibia & Neira 2008; Watson et al. 2013) and trophic studies (appendix 2-3), due to their

numerous trophic interactions with both oceanic and neritic food webs, and to their relatively high consumption rates.

Differing implementations in single areas led to very different results on observed cephalopod impacts on the system (appendix 2-2). In the California Current and in the Bay of Bengal models with different implementation scores indeed showed different impact scores. This shows the impact of both data quality and structural adequacy of a model on its results and the potential conclusions, which has been observed for other predatory groups (Goedegebuure et al. 2017).

Discussion

Considering ecological studies and ecosystem models together led to new insights on the role of cephalopods in our marine ecosystems. Even where models confirm our existing understanding of system functioning, they give useful quantification and allow simulations and predictions helpful for management. Our review of the most adequate models also highlighted the important role of cephalopods in many areas. The wide range of cephalopod trophic relationships and their importance in the diet of many predators (Boyle & Rodhouse 2005, Young et al. 2013), coupled with a strong consumption rate (Coll et al. 2013, Hunsicker & Essington 2013, Alarcón-Muñoz et al. 2008), result in high impact indicators. The key role of cephalopods as a link between lower and upper trophic levels is mainly associated with pelagic or oceanic squids (appendix 2-4). Their wide trophic links with both neritic and oceanic or benthic and pelagic food webs, probably enhanced by their vertical and horizontal migrations, make them a key link between food webs of different habitats. The role of species constrained to the neritic areas thus appears to be more area dependant than those presented in Coll et al. (2013). They have a strong impact on the system in some areas like the south west Atlantic or part of south east Australia, but seem to have a much lesser role in the Bay of Biscay or the North West Atlantic region. Models have been very useful for estimating the different impacts of various cephalopods functional groups.

626 More detailed models could bring new insights on the role of cephalopods in marine ecosystems.
627 Distinction between the pelagic and benthic species (Arancibia & Neira 2008; Gasalla et al. 2010;
628 Markaida & Sosa-Nishizaki 2003; Watson et al. 2013) generally revealed a stronger impact of pelagic
629 groups, except for the Bay of Biscay where both groups have a secondary effect on the system. Many
630 models of the East Pacific regions focused on the jumbo squid (*Dosidicus gigas*) due to its potential
631 negative impact on fisheries resources. This species is an Ommastrephid of high trophic level, feeding
632 on species from trophic level II up to level V, both inshore and offshore (Field et al. 2013; Ibáñez et
633 al. 2015; Markaida & Sosa-Nishizaki 2003; Pardo-Gandarillas et al. 2014; Ruiz-Cooley et al. 2006).
634 The abundance of *D. gigas* has been increasing since the 2000s (Field et al. 2007), and its distribution
635 has extended North and South in a persistent range extension driven by climate changes (Nigmatullin
636 et al. 2001; Zeidberg & Robison 2007). This increase in abundance is believed to be one of the
637 reasons for the depletion of the Chilean hake stock (Alarcón-muñoz et al. 2008), due to the impact of
638 the jumbo squid on its prey (Ehrhardt 1991; Markaida & Sosa-Nishizaki 2003; Rosas-Luis et al.
639 2011). However, these insights do not necessarily converge with ecosystem models results. Several
640 models suggest that the impact of this squid on fisheries resources of the South American region are
641 not critically important (Neira & Arancibia 2013; Taylor et al. 2008), as *D. gigas* predation has less of
642 an impact on Chilean hake than other predators and fisheries that have been overexploiting the stock
643 (Arancibia & Neira 2008; Ibáñez et al. 2008; Arancibia & Neira 2005; Ibáñez 2013). This is probably
644 due to the opportunism of the squid species that are able to feed on various prey in the model, such as
645 mesopelagic fishes (Tam et al. 2008; Taylor et al. 2008). Models strongly suggest that this squid
646 species is sensitive to bottom-up effects that are likely to be the cause of the increase of its abundance
647 after the El Niño period of 1997-98 (Tam et al. 2008; Taylor et al. 2008). However, even if the role of
648 *D. gigas* in the depletion of the hake stock was minor, the strong ecological impact of cephalopods, as
649 suggested in ecosystem models, demonstrates that they could be a factor preventing the hake stock
650 from recovering.
651
652 However, our results on the adequacy of models represent cephalopods collectively suggest there is
653 still a strong limit to our understanding of the role of these species in ecosystems. All values of

keystoneness in EwE are obtained by simulations in which the biomass of the group of interest is changed. The keystoneness is an indicator of the effect of this change on other biomasses. Its robustness thus depends on the adequacy of the representation of ecological processes, directly linked to the quality of data used to build the model and the accuracy of represented mechanisms. This indicator and our impact score are thus much more robust and informative in models of higher implementation score. Confronting the limits of our representation of cephalopods in food webs to their estimated impact in systems shows us that these limits affect our capacity to apprehend global ecosystem functioning. Seven areas showed a model with an impact of cephalopods higher than the implementation score, suggesting a strong uncertainty in the conclusions of these models pertaining to ecosystem functioning and limiting their additional insights on the role of cephalopods. One area had even scores between impact and implementation scores. Five areas had implementation scores higher than their impact scores, suggesting that the global model is robust to cephalopods uncertainties. However, only one of these areas (Bay of Biscay) was marked with an implementation score of at least three. This suggests that most of these results lack robustness and might be changed if local representation of cephalopods is improved. Cephalopods thus have a key, or at least important, role with a widespread impact on the system in many areas, and we highlight the necessity of an improvement of their representation in ecosystem models if we want to draw robust conclusions on their functioning. In South Australia, there are more 'adequate' models (as we have assessed them) available than the one used for our map, but these did not have an index of the impact of cephalopods available (Fulton & Gorton 2014). However, it should be noted that these studies suggested a lesser impact of squids than in Watson et al. (2013) (Watson et al. 2013; Johnson 2011). Only two region (Bay of Biscay and North West Atlantic) appear to have models capable of robust conclusions on cephalopods impact on the system, with an implementation score higher than two and higher than the impact score.

If a poor representation of cephalopods has been previously reported by occasional studies (Hunsicker & Essington 2008; Pedersen & Zeller 2001; Fulton & Johnson 2012), this study detailing the components of their implementation points at the areas requiring improvements. The lack of data and

682 information on cephalopod ecology strongly limits the parameterization of cephalopods in ecosystem
683 models and decreases model robustness. In that regard, the trophic relations of cephalopods are often
684 relatively well documented with diet studies, while data on abundance and biomasses generally lack
685 robustness in the reviewed models. These parameters that lack robustness are often significantly
686 modified after first estimation in order to balance systems that otherwise cannot sustain cephalopod
687 production and consumption (Fulton & Johnson 2012, Shannon et al. 2003, Ullah et al. 2012).
688 However, the quality of data is not the only issue and the inadequate inclusion of cephalopods in
689 terms of model structure further limits the results and conclusions that can be drawn. The distinctions
690 between the various functional groups of cephalopods are seldom made in models, and processes
691 implemented in models are often non suitable to represent cephalopods' life traits. Improving this
692 structure of models could lead to substantial improvements in our understanding of the role of
693 cephalopods in ecosystems. Moreover, improving the structure of models is a relatively easy step
694 compared to the increasing the quality, quantity and spatial resolution of data to inform cephalopod
695 ecology which would likely require comparatively greater time and resources – this should thus be a
696 priority concern for next generation ecosystem modelling studies. In many areas, cephalopods indeed
697 have a strong impact on the system, and the inadequacy and lack of robustness of cephalopods in
698 model representation creates substantial uncertainty in the outcomes of those models. It is possible
699 that where we have assessed the role of cephalopods to be minor, these results are an artefact of the
700 lack of information in the regions and so our assessment of the role of cephalopods in these cases
701 should be interpreted at a minimum level and with caution. Several of these models adjusted their
702 cephalopod parameter(s) to balance the model as the initial system could not sustain the cephalopod
703 consumption required (Chiara et al. 2010; Ullah et al. 2012), suggesting a potentially stronger impact
704 of cephalopods than represented in the final model. Even with these modifications, some of these
705 models still show a strong impact of cephalopods (table 2-4).
706
707 If several modelling studies support the role of oceanic cephalopods as a link between various
708 habitats, many models do not represent cephalopods with enough details to adequately assess this
709 hypothesis, even in areas where trophic studies support it, such as the North West Atlantic (Jackson et

al. 2003; Quetglas et al. 1999), South West Atlantic, Mediterranean Sea (Link et al. 2010; Quetglas et al. 1999) and Atlantic Arctic (Chambers & Dick 2007). Models in these regions either group local squid species together (Barausse et al. 2009; Gasalla et al. 2010; Pedersen & Zeller 2001) or focus only on neritic food webs and species (Pedersen & Zeller 2001). The South West Atlantic is a particular case. In this region, the most adequate model found is focused on the role of the neritic squid *Loligo plei*, when trophic studies also highlight the importance of *Loligo sanpaulensis* or *Illex argentinus* as prey of top trophic levels (Santos & Haimovici 1998; Santos & Haimovici 2000) and predators of lower groups of the food web (Arkhipkin et al. 2012; Cherel et al. 2008). Identifying key species and ecological traits associated with their impact is thus very difficult. The distinction between the different ecologies of many cephalopod species is a relatively simple improvement and should become more common practice. Modellers should also ensure the prey and predators of emerging cephalopod groups are represented as accurately as possible. When there is little knowledge about what are species' role and impact on the food web, the distinction between species of various ecologies could already provide much more robust and valuable results, and allow us to identify any key species. Various traits could be used to segregate species or groups, like habitats (i.e. pelagic, demersal, oceanic, neritic), movements (non-migrating, vertical migrating, horizontal migrating), reproduction (season of spawning, number of cohorts per year), size and others. Differences in diets should also be considered, although in opportunistic species, they would be the reflection of other life-traits differences (i.e. mentioned above) which would be the more accurate marker of distinction.

However, the absence of any model with a structural score of 4 also reflects the inherent inadequacy of model equations and processes used to represent cephalopod life-history traits. The EwE framework as it is often implemented today (as a bulk biomass) can be limited in its capacity to adequately represent cephalopod processes. While inclusion of stanzas can help, it can still be difficult to capture the rapid within season growth rates of cephalopods (though the biomass pool approach allows more freedom on this front than more rigid age structured representations) or their environmental sensitivity, though new model functionality offers a solution to the later issue (Steenbeek et al. 2013). The "senescence" process of cephalopod is also not represented

738 mechanistically, and is key in the population dynamics and turn-over. EwE diets are constrained by
739 the user and do not allow opportunistic diet changes for cephalopods or their predators. Atlantis may
740 capture senescence and other features reproductive features, but without careful thought its diets can
741 also fail to capture the true opportunistic breadth. Moreover, Atlantis was originally conceptualised
742 largely based on yearly cohorts that do not fit many cephalopod species (Jackson & Pecl 2003,
743 Watanabe et al. 2004) which has implications for population dynamics. While the Atlantis framework
744 does offer some opportunities for representing cephalopods' opportunism and exponential growth, or
745 the particularity of their size selectivity, these options are largely hidden from all but the most expert
746 of users and we found very little evidence of their use. The limitations around how cephalopods are
747 represented in models may reflect the lack of data in some regions, but it is likely also due to
748 oversight by modellers who are focused on other parts of the system and who do not appreciate their
749 particularities. As noted above cephalopods have been represented in some of the modelling
750 frameworks not considered here (i.e. OSMOSE in Marzloff et al. 2009) and size based models
751 (Blanchard et al. 2011). However, based on the published documentation of these models we could
752 not find any evidence that these other model types were not prone to the same (or similar) constraints
753 to EwE and Atlantis and so do not provide a ready made solution to the problem of representing
754 cephalopod ecology.
755
756 The relatively simplistic representation of cephalopod functional groups has already been observed in
757 Coll et al. 2013 (Coll et al. 2013). Many models have relatively good data availability (score of 3) but
758 the poor structure of the model (score of 1 or 2) prevents firm conclusions on the role of cephalopods.
759 The main reason for this commonly poor representation of the role of cephalopods is that many of the
760 ecosystem models have been focusing on finfish with simplified handling of invertebrates. The
761 peculiar ecology of cephalopods (with comparatively fast growth and high reproduction rates for
762 species of this trophic level) make their representation in models more challenging using classical
763 representations, especially when data is patchy and poor. The two part nature of these challenges is
764 very important for future work, since improving the structure and algorithmic content of models
765 probably requires less time and resources than the collection and analysis of new data and

766 information, but may be hampered if necessary data is not forthcoming. Consequently, gathering more
767 information on cephalopod ecology should not be disregarded, it would be valuable for improving
768 general understanding as well as model representations.
769
770 The review was not exhaustive. We could only score the role of cephalopods in 23 models from 13
771 regions, mostly from EwE models available on EcoPath database (EcoBase). For an additional 26
772 models, complete results were not available on EcoBase and were not mentioned in related
773 publications, possibly as studies were not necessarily directly focused on the role of cephalopods.
774 Moreover, the validation of the approach against the expert scoring by the small number of model
775 developers who responded to our enquiries suggests that, while indicative, the scoring may have been
776 a little biased in terms of how it judged the impact of cephalopods in systems where the model
777 implementations scores lower. This mismatch is likely due to the limited available information
778 regarding the impact of cephalopods in publications associated with low implementation scores.
779 Nonetheless, the scoring framework used here allows for an assessment of the relevance of a model
780 for answering a particular question (such as the capacity to represent cephalopod ecology) without
781 relying on access to the model developers potentially years later. As confidence indicators like the
782 Pedigree index are too rarely used or published, analysing the origin of the main parameters of each
783 model has been a time consuming process. The impact indicators available for each group available in
784 EwE have also been too rarely used. We could not score the impact of cephalopods in Atlantis models
785 as represented in published studies as clear impact indicators such as the keystoneness index were not
786 regularly provided (typically because the models were focused on specific management questions and
787 performance measures). However, we could assess the adequacy of these models in terms of
788 implementation. The Atlantis framework can incorporate more information on species ecology and
789 potentially allows a more accurate representation of cephalopod processes as it is very flexible for the
790 user (appendix 2-2). Having detailed results available could be very useful for analysis as significant
791 investment is put into model development and implementation, but the majority of the model results
792 are not published in any form and are effectively lost to the broader scientific audience. While it can
793 be argued that potential users could seek permission to access the model directly and run new

794 scenarios, this is not always straightforward as some modelling platforms are difficult and time
795 consuming to use and so ease of sharing in that sense is low (making their output harder to obtain).
796 More readily accessible outputs and results, publicly archived in a similar way as we already do with
797 physical and biological observational data sets, would greatly facilitate the potential for value adding
798 exercises.
799
800 The majority of existing models have strong limitations regarding the representation of cephalopod
801 species, due to a recurrent lack of data and an inadequate representation of their peculiar ecology in
802 modelling frameworks. Models with a relatively more accurate representation of cephalopod ecology
803 provide a different perspective on the functioning of local ecosystems. This emphasises the benefits
804 that could be drawn from an improvement of models capacity to represent these groups, not only in
805 our understanding of their ecology, but also on the global dynamics of ecosystems (table 2-6). The
806 distinction between various functional groups of cephalopods would be a valuable first step. However,
807 an update of core model equations and mechanisms is also necessary if we are to accurately represent
808 ecosystem processes.
809
810

Table 2-6. Key steps and benefits from improving cephalopod representation in ecosystem models.

	Step 1: distinction of various cephalopod groups and ecology		Step 2: representation of new processes to fit cephalopod ecology	
Tools	Parameterization: incorporation of more species specific data.		Parameterization: Incorporation of more ecologically detailed data Modelling: implementation of new mechanisms.	
Examples	Functional groups before	Functional groups after	Mechanisms before	Mechanisms after
	-cephalopod	-oceanic squid -neritic squid -benthic octopus -cuttlefishes	-specified diet -single cohort per year -asymptotic growth	-opportunism -possibility to modulate number of yearly cohorts -exponential growths
	Age distinction before	Age distinction after		
	-no distinction ; Biomass pool gathering all ages.	-several age-groups to represent distinct life stages distributions and		
Benefits and insights	Identification of the various roles and species of importance.		Identification of the ecological traits regulating cephalopod roles and better representation of potential responses to changes.	

It should be noted that the benefits from each step are depending on the availability of data on cephalopod ecology, which probably limits the capacity to successfully complete the step 2 in many regions to this day.

Simulations of climate change scenarios in south east Australia indicate that cephalopods are potential drivers of the response of the ecosystem, as they might be able to buffer the effect of ocean warming and acidification on ecosystem structure (Fulton & Gorton 2014). However, the authors highlighted that the robustness of the implementation of cephalopods was uncertain. On the American west coast, the expansion of jumbo squid (*D. gigas*) distribution raises an important question on their impact on ecosystem functioning. Models in the California Current region do not see jumbo squid as a key species, but their increasing biomass may lead to a change in ecosystem functioning. More adequate models (e.g. with robust data when possible and with distinct cephalopod groups and detailed ecological processes) could determine if the ecosystem conditions could evolve towards a state in which *D. gigas* plays an important role in ecosystem functioning as in the more Southern areas. In the Mediterranean Sea, models have highlighted an increase in cephalopod abundance in ecosystems due to their fast turn-over rates compared to other parts of the food-web (Coll et al. 2006; Coll et al.

825 2008). These cases show the value of ecosystem modelling tools and the necessity of improvements in
826 the representation of cephalopods for ecosystem scenarios and forecasting.
827
828 For this kind of output to have maximal value, however, implementation of cephalopods in ecosystem
829 models would need to be improved. Too few studies represented cephalopods with adequate details to
830 allow us to analyse the ecological processes regulating these roles between various functional groups.
831 This issue is even more pressing in the context of rapid environmental change. The rapid response to
832 environmental change (Pecl & Jackson 2008) and the global increase of cephalopod abundance
833 around the world (Doubleday et al. 2016) should be an incentive to push forward our understanding of
834 the role of cephalopods in ecosystems. Their influence in ecosystem changes has been highlighted in
835 many areas, and models have already provided useful insight on ecosystems changes in the
836 Mediterranean Sea, south east Australia and the American west coast (Arancibia & Neira 2008; Coll
837 et al. 2008; Fulton & Gorton 2014). The depletion of many finfish resources, increase of cephalopod
838 abundance, and a cultural increase in the demand of cephalopods for human diet (Vidal et al. 2014)
839 are probably key factors leading to the increase of cephalopods in fisheries catches. As models still
840 suffer strong uncertainties we cannot draw clear conclusions regarding associated changes in
841 ecosystems subjected to these pressures. This flags foci for future research; as understanding of the
842 role of cephalopods in ecosystem changes could be a key factor in our capacity to develop effective
843 ecosystem based management strategies and buffer or adapt to these changes.

Chapter 3 Understanding the ecological role of cephalopods in the structure and function of ecosystems: a case study using South East Australia.

Abstract

The inability of ecosystem models to represent some of the particular life-history traits of cephalopods has been hampering our capacity to understand their role in food webs and thus to fully comprehend the structure and function of ecosystems. These issues come from a frequent lack of data, but also from the difficulty to represent cephalopod ecology in models originally structured to reproduce the mechanisms of fish ecology. This chapter tackles this issue by focusing on the representation of cephalopod species in the South East Australian ecosystem, a region with a substantial body of literature on cephalopod. We introduce new mechanisms in the Atlantis modelling framework and used all the modelling tools available to represent the particular life-history traits of local species with new accuracy. Squid groups within the model show exponential growth and an ontogenic diet shift; their opportunistic predation allows them to cope with partial reduction in prey availability; and their reproductive dynamics reflects local patterns as they produce several cohorts per year. One of the particularly interesting features of the model is the dependence of arrow squid (*Nototodarus gouldi*) biomass on producer abundance due to their importance in the diet of juvenile squid, and therefore in the recruitment efficiency. Sensitivity tests on growth, assimilation and predation parameters show that the model is strongly sensitive to the representation of the rapid growth process associated with the "live fast die young" life cycle of squids. Ultimately, we reveal the different impacts of the oceanic arrow squid and the

868 neritic calamari (*Sepioteuthis australis*) on the system, largely dictated by their trophic links.
869 Even though the large biomass of forage fish groups in the oceanic habitats substantially
870 buffers any change in oceanic arrow squid abundance or activity, the effect of this arrow
871 squid group on the food web is substantially larger than that of neritic calamari, which is
872 more limited to the neritic groups that are predator or prey of calamari.
873

Introduction

Ecosystem structure and function is influenced by many biotic and abiotic factors, which have various direct and indirect effects and interact with each other (Fulton et al. 2003). The overall understanding of ecosystem functioning and how this may change in the future is thus a demanding challenge. However, although the development of ecosystem models is a great step towards such understanding (Borrett et al. 2014; Sherman et al. 2005), they still suffer from substantial gaps and limitations. The representation of cephalopods in ecosystem models is often highlighted as being particularly difficult (chapter II)(Fulton & Gorton 2014), which is a major limiting factor as these species have an important role in the food web (Coll et al. 2013; Rocha et al. 2001; Smale 1996; Young et al. 2013). Cephalopods occupy all marine zones, oceanic, neritic, benthic or pelagic and are targeted in subsistence, recreational and commercial fisheries in many regions (Arkhipkin et al. 2015; Boyle & Rodhouse 2005). Understanding their role in ecosystems is thus a priority for assessing future changes in the ecosystem and potential management and mitigation of human exploitation.

The importance of cephalopods as a component of fishery catches around the world has been increasing over recent decades until a significant drop in 2016 (Caddy & Rodhouse 1998; Hunsicker et al. 2010) (FAO 2018). This overall increase and strong variability are due to a combination of factors, including a rising interest from consumers, a possible increase in the abundance of cephalopods in the ocean, and the opportunistic nature of fisheries realising that there are marketable alternatives to depleted finfish stocks (Doubleday et al. 2016; Vidal et al. 2014). However, the dynamics of individual commercial cephalopod stocks and populations around the world are renowned for being highly variable. Off the coast of South America for example, at least one cephalopod fishery has collapsed (*Illex argentinus*) while others are growing with the extension of the Humboldt squid (*Dosidicus gigas*) along the west coast of the Americas (Arkhipkin et al. 2015). In the South West Atlantic, cephalopod landings are increasing faster than pelagic and demersal fish

landings (Agnew et al. 2005; Laptikhovsky et al. 2010), although the different species and stocks can have very different life-history and population dynamics (Agnew et al. 2005).

Globally, cephalopods play an important role in ecosystems (Coll et al. 2013)(chapter 1). They are predators of many groups of both low and middle trophic levels (Rodhouse & Nigmatullin 1996), and are an important source of food for many top predators (Smale 1996; Boyle & Rodhouse 2005). Their voracious feeding behaviour and high consumption rate (Rodhouse & Nigmatullin 1996) is correlated with a fast growth at the individual level and a high production rate at the population level (Rodhouse & Nigmatullin 1996; Jackson et al. 2003), making cephalopods a key link between trophic levels of the food web (Cox et al. 2002; Olson & Watters 2003; Griffiths et al. 2010; Field et al. 2013). Assessing the role of these influential groups on food webs is needed to underpin a thorough understanding of the structure and functioning of marine ecosystems (Palumbi et al. 2009). However, the methods used to represent the species of an ecosystem within the model directly impact the results of those models and their responses to perturbations (Goedegebuure et al. 2017).

The need for an ecosystem approach to assess marine ecosystem, resources and functioning has been emphasized over recent decades (Beaumont et al. 2007; Loreau et al. 2001; Sherman et al. 2005). Ecosystem models are now widely developed across the globe allowing analysis of the structure of ecosystems and the complex interactions driving them (Christensen & Walters 2004; Fulton 2010). These tools provide new insights and understanding regarding ecosystem functioning, and allow detailed representation of ecological groups and of the processes driving ecosystem functioning. The most complex representations of ecosystem functioning, end-to-end models, attempt to span the physical, chemical and biological processes at the heart of marine ecosystems (Fulton 2010). They are powerful tools for grasping a broad understanding of ecosystem structures and the indirect impacts of various components on one another. They have been widely used in order to assess the global impacts of human activities on marine ecosystems (Fulton 2010; Haddon 2010; Sainsbury et al. 2000).

927 The important role of some cephalopod families in many ecosystem models has been identified
928 previously (Young et al. 2013). However, these studies are restricted by substantial limits when it
929 comes to a realistic and adequate representation of cephalopod ecology. Despite the impressive
930 potential of ecosystem models, the inclusion of cephalopods in models is often inadequate and their
931 unique life history traits overlooked. Importantly, the diversity of species is rarely represented as all
932 cephalopods are either generally modelled in one mega-group "cephalopods" or split into a pelagic
933 squids group and a more demersal species group that gathers octopods and cuttlefish, or goes so far to
934 subsume cephalopods altogether within a highly aggregated "megabenthos" or "macrobenthos" that
935 includes other large benthic carnivores from very different taxonomic backgrounds (chapter II). The
936 short life-span, fast growth and fast population turn-over of cephalopods has also been a challenge to
937 implement in models (Fulton & Gorton 2014). A critical point to be conscious of is that many studies
938 using commonly implemented ecosystem models treat the cephalopod parameters (eg biomass, diet,
939 consumption and/or productivity) as a means of balancing the overall model (Shannon et al. 2003;
940 Ullah et al. 2012). While acceptable within the guidelines of adjusting the most uncertain parameters
941 first, it likely does not do the group justice; making their modelled ecological characteristics more an
942 artefact of the parameterization process than a faithful reproduction of their ecology. This obviously
943 limits the conclusions which can be drawn from the models when it comes to understanding the
944 ecosystem role and influence of cephalopods. While adding details and complexity to models does not
945 necessarily improve model performance (Fulton 2001), it is important to capture fundamental
946 dynamic dictating features and it is clear that the relatively poor implementation of cephalopods
947 (chapter II) needs to be addressed to adequately consider the complexity, and the importance of their
948 ecology and impact on other food web components.
949
950 Here, I aim to clarify the ecological role played by the various cephalopod species in an otherwise
951 reasonably well-understood system, and to identify the ecological processes involved in the regulation
952 of that ecological role. I first adapted an existing ecosystem model, so that it had a strong focus on the
953 ecology of cephalopods. I used an Atlantis model (SEAP) of the South East Australian (SEA) region
954 that has been regularly updated over the last decade (Fulton et al. 2007; Fulton & Johnson 2012;

Fulton & Gorton 2014). As in many studies, the conclusions of the South East Australian suite of models have high degrees of associated uncertainty, particularly regarding the dynamics of the invertebrate groups, due to the representation of the cephalopod groups (Fulton & Gorton 2014). This is despite the area being the focus of many previous studies in the region on many different aspects of cephalopod ecology on a suite of the key species (Aitken et al. 2005; André et al. 2009; Doubleday et al. 2006; Dunning & Brandt 1985; Jackson & Pecl 2003; Lansdell & Young 2007; Norman & Reid 2000; Pecl & Moltschaniwskyj 2006). Recent model studies indicated that the group was critical to nearshore ecosystem dynamics (Watson et al. 2013). I thus modified the base model to represent more accurately the ecology of various cephalopod species of the region.

The key elements in terms of appropriate representation of cephalopods in the ecosystem model were then identified with a sensitivity analysis. Sensitivity analysis is a powerful approach to not only to identify the optimal parameterization during the calibration processes, but also to test assumptions underlying the representation of the system and to assess the system response to changes (Fennel et al. 2001). I then compared the results of the SEAP model under various combinations of cephalopod parameters and processes. This ultimately allowed the identification of effective representations of cephalopods – i.e. what processes and life history traits must be captured to produce dynamics closest to what has been observed in nature. In that way the life history traits that are most likely involved in the regulation of the role of cephalopods in the system can be identified and a greater understanding gained of cephalopod ecosystem ecology.

Material & methods

The single group representing different families of squid in the base model was replaced by three groups representing species of very different ecologies. I also divided predator groups due to their different links with various squid families and modified the ecological mechanisms represented in Atlantis to allow us a more accurate representation of the peculiar ecology of cephalopods. I then

assessed the relevance of the changes made by testing the sensitivity of the system to the parameters of the different squid groups.

Preliminary ecosystem model of South East Australia

Atlantis is a modelling framework allowing a representation of the whole biogeochemical ecosystem - an end to end deterministic model (Fulton et al. 2011). The physical environment is represented by a division of the geographical area of interest into horizontal polygons and vertical layers. The biophysical sub-model tracks the flows of nutrients (nitrogen in our case) through the biological groups in a system resolved in three dimensions. The food web is built on functional groups that are subjected to key ecological processes that include their consumption, production, migration and recruitment. Movements between polygons and layers are represented by advection or migration. Anthropogenic components represent human impacts on the system, generally focusing on specific fisheries and associated management dynamics. The implementation of all these components is subject to a wide range of options, and further information can be found in other studies (Fulton, Smith, et al. 2004; Fulton, Parslow, et al. 2004, Fulton et al (2011).

The modular construction of Atlantis allows for the implementation of system components and groups with various levels of details or simplicity. Lower trophic levels and invertebrates like cephalopods, are generally represented as biomass pools (potentially with separate juvenile and adult pools), while vertebrates are implemented in age-structured groups. By adapting the Atlantis toolbox I have improved the implementation of cephalopod species in several important ways (see next sections). For example, until now, all groups with explicit spawning have been set to reproduce once per year. I modified the Atlantis demographic calendar to allow for multiple spawning events per year, based on the biology of the species in question.

Here I use the Atlantis-SEAP model (from South East Adaptation Program), originally developed by Johnson (2011). The model extends from the central South Australian border to the New South

Wales-Queensland border and encompasses the Tasmanian shelf and Tasman Sea in the South (fig 3-1). The model uses a telescoping spatial structure to maximise geographic details around fine scale coastal features, such as small-sized marine protected areas and crucial habitats (e.g. reefs; Johnson et al 2011).

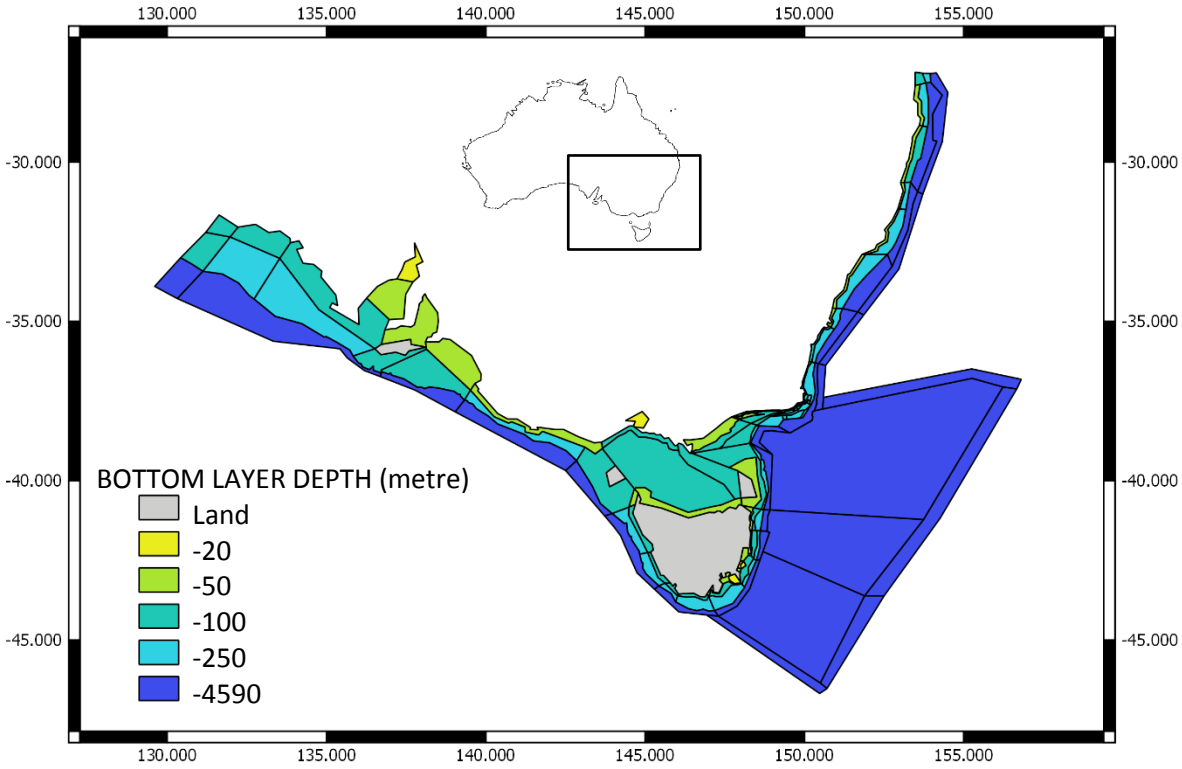


Figure 3-1. SEAP model area and spatial divisions.

Focus on cephalopod groups and processes in the South East Australia

New food web structure

The SEAP model was originally built to cover the main ecological groups in the region, especially species of interest for fisheries or species assessed as vulnerable to climate change (Fulton & Gorton 2014; Pecl et al. 2011). However, the explicit representation of cephalopod groups were limited to an aggregate "Commercial squids" group which represents both arrow squid (*Nototodarus gouldi*) and southern calamari (*Sepioteuthis australis*) (table 3-1). Demersal cephalopods were folded into the

1025 generic macrozoobenthos groups. I divided cephalopods into more highly resolved functional groups,
1026 and also further divided some key fish predator groups based on their different links to the now
1027 distinct cephalopod species groups.

1028 **Table 3-1. Functional groups and species included in the model.**

Group Name	Group composition	Model abbreviation
Aquaculture Salmon	*Salmo salar*	AQS
Aquaculture Tuna	*Thunnus maccoyii*	AQT
Aquaculture Oysters Mussels and Abalone		AQM
Aquaculture Prawns	*Penadeus monodon*	AQP
Large planktivorous fish	*Trachurus declivis, Scomber australasicus, Emmelichthys nitidus, Trachurus novaezelandiae*	FPL
Blue grenadier	*Macruronus novazelandiae*	FBG
Small planktivorous fish	*Sardinops sagax, Engraulis australis, Hyperlophus vittatus, Spratelloides robustus, Trachurus novaezelandiae, Argentina australiae*	FPS
Ocean plank/pisc fish	Exocoetidae, Scomberesocidae	FVD
Banded morwong	*Cheilodactylus spectabilis*	FBM
Shallow piscivorous fish	*Arripis trutta, Thyrsites, Dinolestes lewini, Arripis georgianus, Pomatomus saltatrix, Sphyraena, Euthynnus affinis, Atractoscion aequidens, Sarda australis, Coryphaena hippurus, Argyosomus hololepidotus, Seriola lalandi*	FVS
Shallow demersal reef fish	*Trachinops caudimaculatus,* Labridae, Monacanthidae, *Atypichthys latus, Scorpis aequipinnis, Enoplosus armatus, Caesioperca lepidoptera, Pempheris multiradiata, Scorpis lineolata*	FDR
Large piscivorous fish	*Auxis thazard, Katsuwonus pelamis, Thunnus, Istiophoridae, Xiphias gladius, billfish*	FVT
Epipelagic fish feeders	***Auxis thazard, Thunnus albacares, Kadjikia audax***	FTE
Mesopelagic fish feeder	***Thunnus alalunga, Xiphias gladius***	FTM
Flatheads	Platycephalidae	FFH
Migratory mesopelagics fish	Myctophids	FMM
Non-migratory mesopelagics fish	Sternophychids, cyclothene (lightfish)	FMN
Purple wrasse	*Pseudolabrus fucicola*	FBP
Deep demersal fish	Zeidae, Cyttidae, *Genypterus blacodes, Rexea solandri, Polyprion oxygeneios, Paraulopus nigripinnis, Rexea antefurcata, Coelorinchus, Oreosomatidae*, Macrouridae, Zenopsis, Centroberyx, cardinalfish, *Mora moro*	FDD
Shallow demersal herbivores	Kyphosus sydneyanus, Girella elevata, Hyporhamphus melanochir, Girella tricuspidata, Dactylophora nigricans, Aplodactylidae, Mugilidae	FDH
Other shallow demersal fish	Paralichthyidae, Pleuronectidae, Triglidae, Rhabdosargus sarba, Pseudophycis bachus, Lotella, Pseudophycis, Acanthopagrus butcheri, Pseudocaranax georgianus, Acanthopagrus australis, Sillago, Zeus faber, Helicolenus percoides, Hime purpurissatus, Batrachoidiformes, Nemadactylus, Sebastes alutus, Pterygotrigla, Uranoscopidae, Scolecenchelys breviceps	FDS
Magpie perch	*Cheilodactylus nigripes*	FDM
Shallow territorial demersal fish	Hippocampus, *Phycodurus eques, Phyllopteryx taeniolatus*, Stigmatopora, Gobiidae, Pomacentridae, *Monodactylus argenteus*	FDT
Herring cale	*Odax cyanomelas*	FHC
Blue throat wrasse	*Notolabrus tetricus*	FBW
Pink snapper	*Pagrus auratus*	FSN
Warehous and trevalla	*Seriolella, Hyperoglyphe Antarctica*	FWT

Striped tuna	*Katsuwonus pelamis*	FST
Green eye dogfish	*Centrophorus*	SHG
Demersal sharks	*Heterodontus portusjacksoni*, Scyliorhinidae, Orectolobidae	SHD
Spiky dogshark	*Squalus megalops*	SHS
Pelagic sharks	*Prionace glauca, Isurus oxyrunchus, Carcharodon carcharias, Carcharhinus*	SHP
Gummy shark	*Mustelus antarcticus*	SHR
Skates and rays	Rajidae, Dasyatidae	SSK
Seabirds	Diomedeidae, *Puffinus*, Laridae, *Morus, Eudyptula minor*	SB
Urchins		BGU
Pinnipeds	*Arctocephalus pusillus doriferus, Arctocephalus forsteri*	PIN
Abalone	*Halioteuthis laevigata, Halioteuthis rubra*	BGA
Baleen whales	*Megaptera novaeangliae, Balaenoptera, Eubalaena australis*	WHB
Dolphins	Delphinidae	WHS
Orcas	*Orcinus orca*	WHT
Lobster	*Jasus edardsii, Jasus verreauxi*	BRL
Squid	*Nototodarus gouldi, Speioteuthis australis*	CEP
arrow squid	***Nototodarus gouldi***	NGO
Oceanic squids	***Ommastrephes bartramii, Todarodes filippovae, Stenoteuthis oualaniensis***	OMM
Southern calamari	***Sepioteuthis australis***	SQN
Cuttlefishes	***Sepia apama***	CUT
Octopods	***Octopus pallidus***	OCT
Gloomy octopus	***Octopus tetricus***	OCM
Other benthic filter feeder	mussels, oysters, sponges, corals	BFF
Deep benthic filter feeder	holothurians, echinoderms, burrowing, bivalves	BFD
Macrozoobenthos	stomatopods, asteroids, gastropods, crustaceans	BMD
Crabs		BMS
Prawns		PWN
Carnivorous zooplankton		ZL
Deposit Feeder		BD
Macroalgae	Kelp	MA
Seagrass		SG
Benthic Carnivore	Polychaetes	BC
Gelatinous zooplankton		ZG
Diatom		PL
Pico-phytoplankton		PS
Mesozooplankton	Copepods	ZM
Microzooplankton	Flagellates	ZS
Pelagic Bacteria		PB
Sediment Bacteria		BB
Meiobenthos		BO
Labile detritus		DL
Refractory detritus		DR
Carrion		DC

1029 The groups removed from the previous model are shaded red and those in green are new additions to the model.

The new representation of cephalopods is based on several ecological criteria (table 3-2). The main ecological differences between groups are based on trophic and habitat studies. To identify cephalopod species of importance in the food web, I reviewed the literature on diets of local predators. Each species occurring frequently in diets is represented by a functional group in the model. The distinction or aggregation of species in groups was based on the available information in diet studies and on the various habitats of each species, giving us insights on the distinct ecological niches of the different groups (table 3-2, appendix 3-1). Species of interest for fisheries and species that have already been observed to respond to climate change were also represented in different groups as pressures associated with these groups impact ecosystem functioning. These groups could potentially drive ecosystem changes, or could be regarded as useful indicators of ecosystem changes.

The most extensive information was available on the neritic squids *N. gouldi* and *S. australis*, the cuttlefish *S. apama* and the octopus species *O. pallidus.* These species were the focus of many ecological studies in this area (appendix 3-2), which allowed a relatively robust parameterization. These species are represented in the model as they are targeted recreationally and commercially or important resources for various fisheries. The arrow squid is targeted by the Southern Squid Jig Fishery, and is an important catch of the Commonwealth Trawl Sector and the Tasmanian Scalefish Fishery. The calamari is an important target of the South Australia Marine Scalefish Fishery and the Tasmanian Scalefish Fishery. *Octopus pallidus* is the focus of the Tasmanian Octopus Fishery. The cuttlefish species are mainly targeted by recreational fisheries, which occasionally record catches higher than some professional cephalopod fisheries (Hall & Fowler 2003). The *Octopus tetricus* is mostly caught as a by catch of octopus fisheries and other fisheries, but is set up as an separate group as it has been observed to undergo a range-shift following the perturbation of the environmental conditions (Ramos et al. 2015).

Collectively, the cephalopod species span many different ecological traits (table 3-2) and thus need to be represented by a new suite of distinct functional groups. I used the abundance of various

cephalopod species in predator diets to identify more appropriate groupings and where the trophic resolution needed to be increased. These diets provide insights about the relative importance of various species in the food web (appendix 3-2). Oceanic squids (*Todaropsis eblanae*, *Ommastrephes bartramii*, *Onykia robsoni*) appear to be a significant component of the food web. These species are grouped into one single group, as they have similar life history traits and distribution. Most of the parameters of this group are based on *O. bartramii* as it appears to be the dominant species of oceanic squid (by biomass) in the South East of Australia (Dunning & Brandt 1985). It is also a species on which significant research has been done (Bower & Ichii 2005).

Table 3-2. Features of the various cephalopod groups in our model. Fisheries catches are the catch range between 2000 & 2013 in whole South East Australia. See Appendix 3-2a and 3-2b.

	Distribution	Abundance	Main trophic links (by order of importance)	Movement	Reproduction	Fisheries catch range (between 2006-2015)	Environmental sensitivity
arrow squid (*N. gouldi*)	Neritic	From fisheries, surveys, trophic links and model calibration	Prey: fish (myctophids, lightfishes, clupeids), squids (Gould, ommastrephids), planktonic crustaceans.	Diurnal feeders at surface, nocturnal demersal dwellers	Each individual spawns for one month before senescence.	330-2500t	Faster growth in warmer waters
	Pelagic 0-500m depth		Predators: seals, dolphins, tunas		New cohorts all year round with 4 peaks per year		
Oceanic squids (mainly based on *O. bartramii* ecology)	Oceanic	From trophic links and model calibration	Prey: fish (myctophids), cephalopods (ommastrephids, histioteuthids, octopods), crustaceans.	Nocturnal surface hunter, diurnal demersal dwellers	Two spawning months per individuals	none	Faster growth in warmer waters
	Pelagic 0-1500m depth		Predators: seabirds, tunas		Two cohorts per year: autumn and winter-spring		
calamari (*S. australis*)	Neritic	From fisheries, trophic links and model calibration	prey: fish (clupeids, mackerel), octopus, squid, megabenthos	Neritic reproduction migration	One spawning month per individuals	480-620t	Faster growth in warmer waters
	Demersal		Predators: pinnipeds, sharks, dolphins		New cohorts all year round with early summer peak		
Giant cuttlefish (*S. apama*)	Neritic	From fisheries, trophic links and model calibration	Prey: crabs, shrimps, small fishes	Reproductive aggregation	One spawning month per individuals	1994-2000: 15-260t	Faster growth in warmer waters
	Demersal		Predators: pinnipeds, sharks		Winter spawning		
Pale octopus (*O. pallidus*)	Neritic	From fisheries, trophic links and model calibration	prey: crustaceans (megabenthos), molluscs (filter feeders), octopus, polychetes, clupeids	Benthic only	One spawning month per individuals	40-120t	Faster growth in warmer waters with limit at 27°C

	Benthic		predators: sharks, demersal and benthic fishes		Late summer early autumn spawning		
Gloomy octopus (*O. tetricus*)	Neritic	From fisheries, trophic links and model calibration	prey: crustaceans (megabenthos), molluscs (filter feeders), octopus, polychaetes	Benthic only	One spawning month per individuals		range shift poleward
	Benthic		prey: crustaceans (megabenthos), molluscs (filter feeders), octopus, polychaetes		New cohorts all year round with peaks in summer and autumn		

Note: The catch range is the minimum and the maximum catch from 2000 to 2013 (fish.gov.au).

Note: I considered increasing the length of spawning events of calamari to 2 months (Jackson & Pecl 2003; Pecl 2001; Pecl & Moltschaniwskyj 2006), but the structure of the model would not allow it, likely due to the overlap of resulting reproduction periods. I considered the representation of age structure with several cohorts and spawning events per year a priority over the increase of the spawning period.

I could gather a significant body of literature on many cephalopod species of the region (appendix 3-1). However, for the oceanic Ommastrephid group, little information was available for the model area. For some processes, I thus used studies on the *O. bartramii*, the dominant species of this group (Dunning & Brandt 1985), from the North-West Pacific where there was a lot of information. This geographic distribution of the studies is likely due to the differences of interest in these species from fisheries. For groups that were in the original SEAP model, parameters from the previous version of the model (Johnson et al. 2011) were double checked with recent studies and updated when needed and possible. The life history traits of most of the cephalopod species could be found in local studies (appendix 3-2).

Focus on cephalopods ecology and new processes represented

As I built the model representation of the cephalopod functional groups, I focused on representing their particular ecology (Table 3-3); either using the options in Atlantis that best represented these features, or developing and implementing new processes to model their movements, growth, reproduction and feeding behaviour. The modular structure of Atlantis compared to other modelling frameworks was key to allow us to incorporate these processes fitting cephalopod ecology.

Table 3-3: Improvements on ecological processes of cephalopods. See appendix 3-1 for supporting studies.

Model processes	Base model	New model	Comments and ecological processes impacted	Change significance
Reproduction strategy	One cohort per year	Several overlapping cohorts per year	Represent the conveyor belt of recruits of some species	***
Age structure	Juvenile/adults distinction	Up to 4 cohorts	Exponential growth Ontogenic diet shift	**
Stock-recruitment relationship	Linear relationship	Beverton-Holt relationship	Increased variability & recovery capacity, density dependence effect	**
Feeding	Prey size has to be inferior to 40% of cephalopods size	Preference for prey inferior to 80% of cephalopods size, and occasional bigger prey	Wider prey range	**
Vertical migration	No movements	Vertical diel and diurnal migrations	Feeding and foraging movements	**
Horizontal migration	No movements	Horizontal seasonal migrations	Spawning migrations	**
Prey species		Group specific		*
Growth rate		Group specific		*
Assimilation		Group specific		*
Distribution		Group specific & updated		*
Habitat		Group specific & updated		*
Senescence				

Change significance	
***	Implementation of new functions to represent ecological traits not previously represented (to our knowledge).
**	More accurate representation of a process with a modelling option unused for cephalopods before (to our knowledge) – e.g. alternative non-linear stock-recruitment relationships, different size selectivity of prey.
*	Improvement of the process representation due to the distinction of different ecological groups. New, more accurate, Parameters are defined for each group.

	Process already represented.

The previous aggregation of oceanic and neritic or benthic and pelagic species in models often prevented any relevant representation of their distribution or movements. For each species, seasonal migrations to specific spawning grounds (Hall & Fowler 2003; Moltschaniwskyj & Pecl 2007) are implemented with a specified seasonal distribution across the boxes. The vertical feeding migrations (Uozomi et al. 1995; Voss 1967) are simulated by a differentiation between day and night in the vertical distribution of groups among the model's layers. The use of a new age structure for cephalopod groups also allowed us to represent various processes in more detail. I distinguish four age classes, from juveniles to matured adults, to allow for a more useful parameterisation of the exponential growth of cephalopods (Chen & Chiu 2003; Leporati et al. 2008; Pecl 2004; Semmens et al. 2004) and an ontogenic shift of the diet.

The capacity of cephalopods to feed on relatively large prey thanks to their feeding apparatus was represented with a new feeding process and new parameters (Appendix 3-1). The Atlantis framework offers the possibility of limiting the size of prey, and to scale the amount of prey available based on their size compared to the predator's size. I could thus represent cephalopod groups feeding on prey that are relatively large in comparison to the prey groups of most other groups in the system. One of the main new features of our representation of cephalopod ecology is the representation of several spawning events per year for the population (Appendix 3-1). This process is not represented for explicitly size and age structured cephalopod groups in other ecosystem models to our knowledge. This is because biomass pool models (e.g. Ecopath with Ecosim; Christensen & Walters 2004) do not represent explicit reproduction events when not distinguishing life history stanzas (amalgamating individual and population level growth), while more detailed models (i.e. Osmose and Atlantis; Shin & Curry 2004; Fulton et al. 2005) rely on a representation of the aging process that is based on yearly cohorts only. It is possible to capture the annual reproductive strategies of cephalopods using stanza representations in Ecopath with Ecosim but to the authors' knowledge that has not yet been done in a published model. The previous versions of the SEAP model included stage structured cephalopods

(distinction between juvenile and cephalopods), but this was a simplistic annualised biomass pool representations that I felt was insufficient, as annual cohorts do not adequately represent the implications of having several spawning events and cohorts per year (Green 2011; Jackson et al. 2005; Steer et al. 2007; Ichii et al. 2004; Jackson et al. 2003). I thus implemented new routines in Atlantis to allow for the parameterisation of groups with more than one spawning and recruitment per year (fig 3-2). It should be noted that despite the acknowledgement of multiple spawning occurring in individuals (Pecl 2001; Rocha et al. 2001), they are usually only represented as spawning once in their life within the model, as these spawning events occur in a relatively short period of time and computation complexity grows rapidly if individual spawning events must be tracked per individual. Even with this constraint, the more resolved representation also allowed us to represent the phenotypic variability in the expression of ecological characteristics across cohorts due to the different environmental conditions they experience (Ichii et al. 2004; Triantafillos 2002).

Table 3-4: marking of model adequacy to assess cephalopods (chapter II).

		Structural Implementation			
		1	2	3	4
data quality	1	I	II	II	II
	2	II	III	III	III
	3	II	III	IV	IV
	4	II	III	IV	V

Base model | New model

Processes impacts and model sensitivity to cephalopods uncertainty

While the structural improvements addressed one source of model uncertainty – structural uncertainty- parametric uncertainty cannot be ignored. As cephalopods are known for the variability of their ecology, I conducted a sensitivity analysis on their parameters. I focus on their life-history traits that generally express the strongest uncertainty and variability – their growth (Jackson et al. 2003; Semmens et al. 2011), reproduction (Steer et al. 2007) and diet (Pethybridge et al. 2012) (table 3-5a). I tried to identify the key processes that regulate the impact of cephalopods on the model, and to assess the robustness of the model to that specific parametric uncertainty. To assess the robustness

of the model and the impact of various processes, I compared the results of various parameterizations, considering the changes in numbers and size of cephalopods, and the changes in biomass of other groups.

The fast growth of cephalopods sets them apart from most of other predators of the system, who usually have slower and longer life-cycles. The variability of this growth among cephalopods, in space and time, is very important. I therefore tested model sensitivity to food intake and the assimilation efficiency. The Atlantis framework offers several alternative feeding functions, which can be tailored predator to predator. Among these options, the Holling-type II equation (Murray & Parslow 1999), which is often a preferred implementation, was chosen as Fulton et al. 2003 determined that alternative functions required additional parameterization but resulted in similar results.

$$Grprey = \frac{B.C.Bprey}{1 + \frac{C.\sum_i (Ei.Bprey,i)}{mum}}$$

Predator feeding is based on the biomass of predator and the biomass of prey (B), the search capacity (called "C" in the Atlantis framework), the assimilation efficiency (called "E" in the Atlantis framework), and the maximum growth rate (called "mum" in the Atlantis framework). The analysis was focused on the maximum growth rate (Table 3-5b) and assimilation efficiency (Table 3-5b).

The opportunism of cephalopods is a complicated trait to represent in models. However, the predation model of Atlantis allows the user to attempt an implementation. The availability of prey is based on the probability of encounter and the relative size of the predator and prey. The amount of available prey is then scaled with a "preference" parameter to estimate the quantity of prey actually attacked (table 3-5b). This parameter is usually calibrated for each prey group in order to have an emergent realised diet similar to local observations. This "preference" (or "availability") is a highly uncertain parameter that cannot be easily measured and requires careful attention and alternative parameterisations. The prey preference parameters for the cephalopod groups was initially set at the maximum for all prey groups, to represent their opportunism - as any encounter of a potential prey would result in an attack. However this approach needed to be adjusted as it resulted in diets based on

primary and secondary producers (e.g. plankton groups) for all cephalopod groups, which is unrealistic. The preference/availability of the invertebrate groups was thus downgraded to account for unrepresented hunting processes and I only kept prey preference at the maximum for the structured groups (i.e. fish and sharks) present in cephalopods diets, as more of those hunting processes are explicitly represented through model mechanisms estimating encounter rates. The impact of a change of voracity of cephalopod species on oceanic fishes, on neritic fishes, on crustaceans and on all these groups together was tested.

Table 3-5a. Various sensitivity tests

Parameter targeted	Voracity				Growth rate		Assimilation	
Test number	2	3	4	5	6	6	7	8
Change amplitude	a-j	a-j	a-j	a-j	a-e	f-j	a-j	a-e
Change	Decrease				Decrease	Increase	Decrease	Increase
	On all prey	On oceanic fish	On neritic fish	On crustaceans				

All those tests are run on arrow squid (NGO) and calamari (SQN). The names or code of each run reflect the species and parameter targeted, and the amplitude of the change (i.e. NGO6a is a relatively small decrease in growth rate of arrow squid, and SQN8e is a strong increase of the assimilation rate of calamari). The following tables cover each test in more details.

Table 3-5b: Method used to build tests on squid parameters.

Method used to build tests for maximum growth rate parameter

Test 6	Standard		Change amplitude									
			decrease					increase				
	Cohort		a	b	c	d	e	f	g	h	i	j
			-10%	-20%	-30%	-40%	-50%	+10%	+20%	+30%	+40%	+50%
	1	*16.84*	*5.47*	*4.10*	*2.74*	*1.37*	*0.68*	*8.20*	*9.58*	*10.94*	*12.31*	*13.68*
	2	*11.4*	*9.12*	*6.84*	*4.56*	*2.28*	*1.14*	*13.68*	*15.96*	*18.24*	*20.52*	*22.8*
	3	*57*	*45.6*	*34.2*	*22.8*	*11.4*	*5.7*	*68.4*	*79.8*	*91.2*	*102.6*	*114*
	4	*67*	*48*	*36*	*24*	*12*	*6*	*72*	*84*	*96*	*108*	*120*

Method used to build tests for maximum assimilation rate parameter

Test	Standard	Change amplitude									
		a	b	c	d	e	f	g	h	i	j
7	*0.8*	*0.76*	*0.72*	*0.68*	*0.64*	*0.6*	*0.56*	*0.52*	*0.48*	*0.44*	*0.4*
8	*0.8*	*0.82*	*0.84*	*0.86*	*0.88*	*1*	-	-	-	-	-

Method used to build tests for voracity parameter

Test	Standard	Change amplitude									
		a	b	c	d	e	f	g	h	i	j
2,3,4,5	-	-10%	-20%	-30%	-40%	-50%	-60%	-70%	-80%	-90%	-99%
	1	*0.9*	*0.8*	*0.7*	*0.6*	*0.5*	*0.4*	*0.3*	*0.2*	*0.1*	*0.01*
	← Opportunistic voracious behaviour when this prey is present.				Prey is easy to capture and is eaten relatively often.						→ Prey "unliked" or difficult to capture; they are eaten when other prey are unavailable.

The actual values (in italic) are examples taken from the parameters of the model.

The example for growth rate tests are from the arrow squid parameters (in $g.d^{-1}$); the values for assimilation are common between arrow squid, calamari and ommastrephid species; the values for the voracity parameter are

different for each link between cephalopod group and its prey, I thus used an example with high prey preference which was used for most prey of cephalopod to reflect their voracity. Note that the maximum growth rate corresponds to a theoretical growth grate of a fast growing individual in conditions ideal for its growth. This is not a parameter truly observable in field studies, but its importance to model behaviour makes it of interest in these sensitivity tests.

For comparison: Most fishes have an Efficiency of 0.2 to 0.5 and top predators have an efficiency of 0.4 to 0.8.

Sensitivity analysis is a powerful not only for identifying best fit (or at least constraining to feasible data) parameterizations during the calibration process, but also for testing assumptions underlying the representation of the system and to assess the system responses to change (Fennel et al. 2001). To assess the system-level effects of the changes to squid parameters, I ran principal component analysis (PCA) on the simulation end-state results (i.e. relative change in biomass of each functional group after 40 years of simulation time) for the different tests. Using the average biomass change over the last 5 years or the change at other specific time periods after the model burn-in period did not make a significant difference to the PCA results, which is the reason why the discussion is constrained to the end-state results here. I analyse and describe the output and significance of those tests further by looking at changes on group biomasses, growth or diets. The R version 3.4.3 and the package "ReactiveAtlantis" was used.

Results

Analysing results from new ecological representations

Effects of the new population dynamics on cephalopod groups

Our biomass trends show different rhythms and patterns for each species (fig 3-2a). The arrow squid biomass has four peaks per year, with significantly stronger peaks around June and September, during the autumn-winter periods. These stronger peaks are about 60% higher than the smallest peaks occurring around summer season. The Ommastrephid biomass has two peaks per year around the end of January and the end of August. The calamari group has a biomass with four peaks per year, and

relatively little variability each season. Higher peaks, occurring in March-June, are about 30% higher than smaller peaks, around the end of November.

The trend of arrow squid and Ommastrephid biomasses are significantly correlated with the abundance of zooplankton and large phytoplankton (correlation coefficient of 0.496001; using the Pearson correlation test with R 3.3.2) (fig 3-2b).

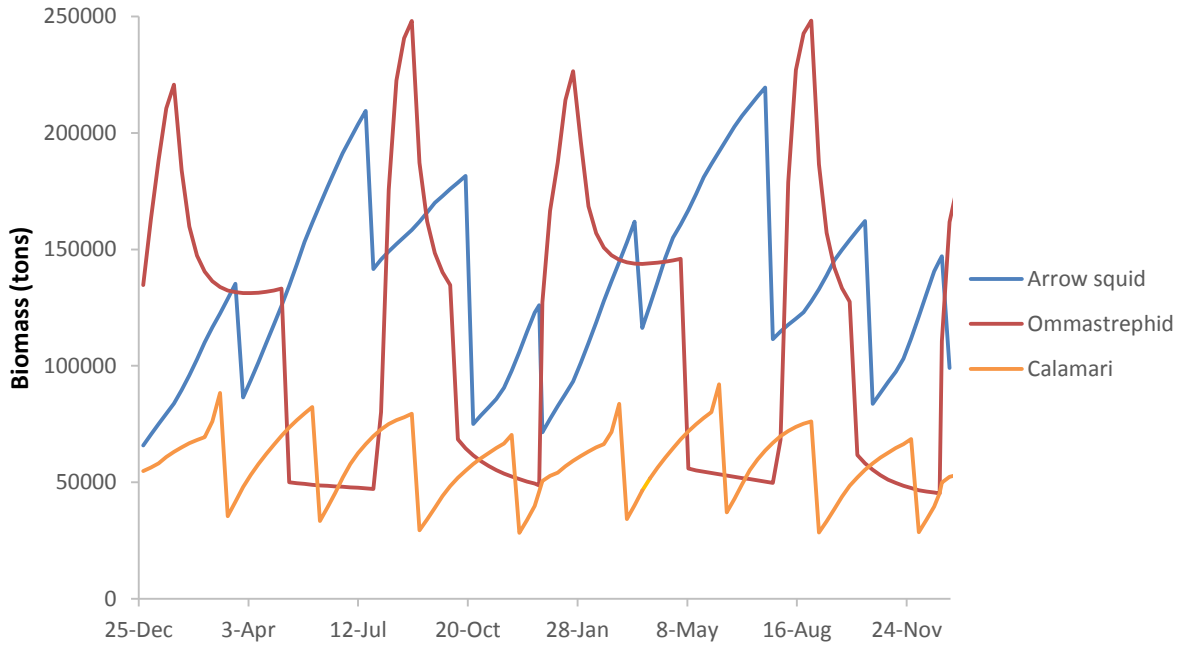


Figure 3-2a. Biomass trend of squids.

These trends are taken after 25 years of run, about ten years after the model reaches a balance.

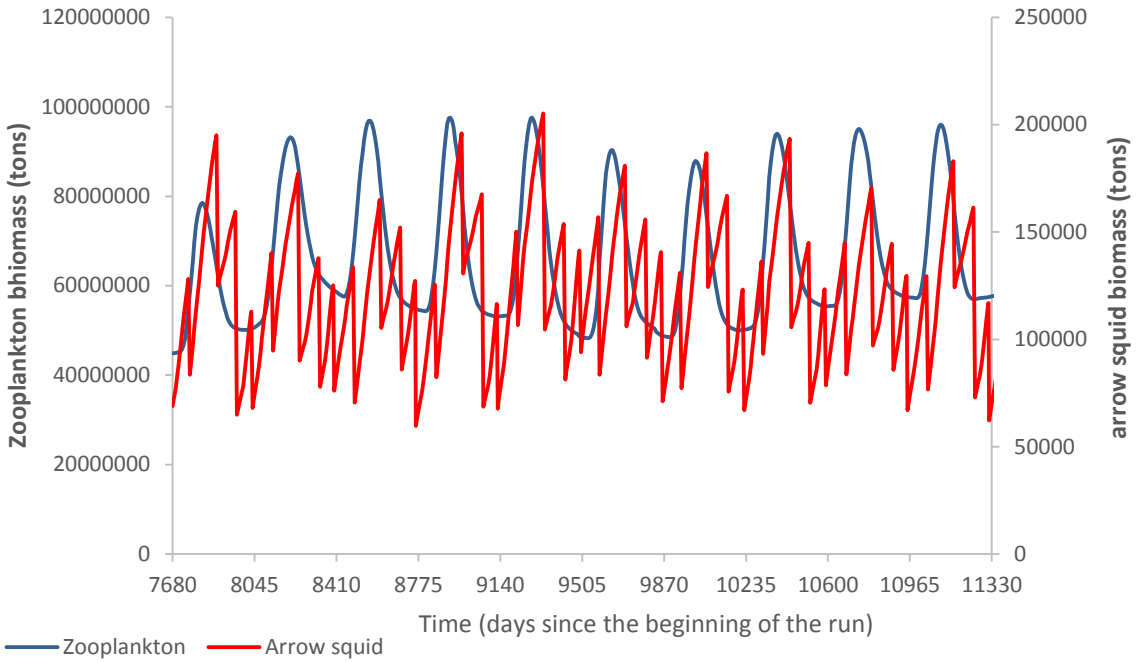


Figure 3-2b. Biomass trends of arrow squid and large zooplankton over the last ten years of our base run.

Effects of the new growth and diet dynamics on cephalopod groups

Each life stage of the three squid species had a different set of prey (fig 3-3). The first stages (stage 1 and stage 2), are immature stages during which squid feed mostly on zooplankton and crustaceans. There is then a shift towards fish species that constitute about 40% of the adults' diet. The definition of various life stage allowed us the parameterization of an exponentially increasing weight of squids (fig 3-4). Arrow squid grow exponentially from about 50g for the first individual considered in the age structure up to almost one kilogram for the biggest individuals.

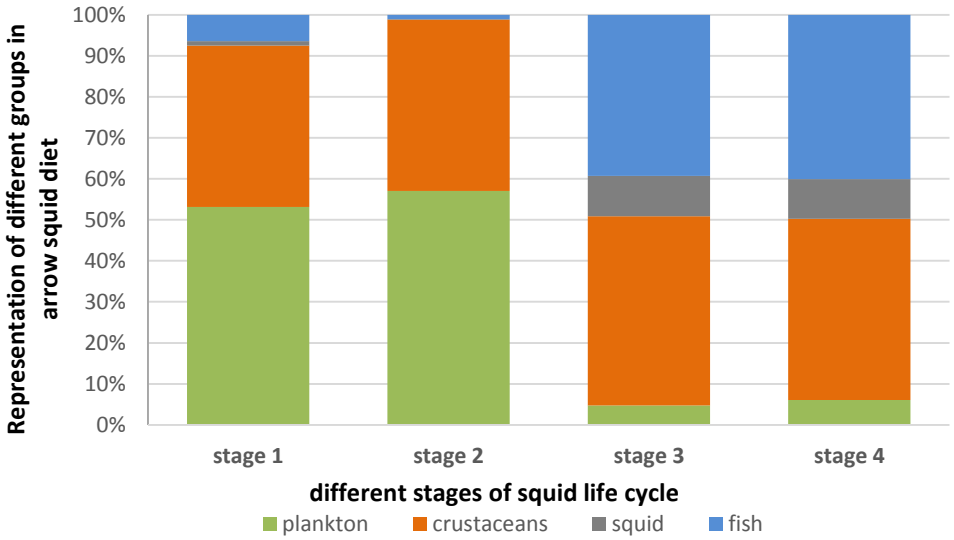


Figure 3-3. Changes of diet across the different stages of arrow squid.

These diets are taken from the standard run after the calibration time.

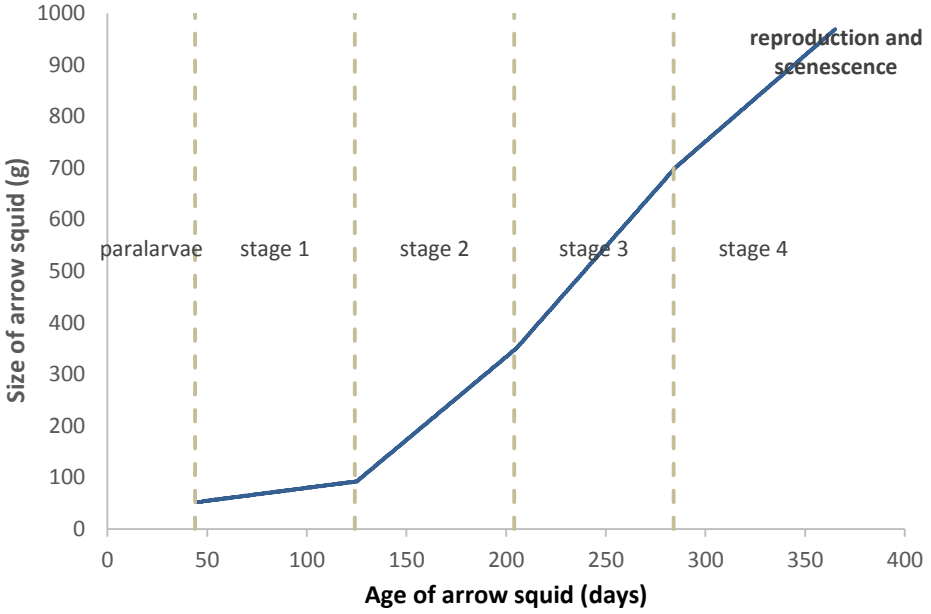


Figure 3-4. Exponential growth of arrow squid.

This growth curve is based on the size of the biggest individuals in the standard model, after the calibration time.

Sensitivity tests

General assessment of the impacts of changing squid parameters

The results extracted from models with forced changes on calamari (SQN) clearly stand out from the results from models with forced changed on arrow squid (NGO) (fig 3-5). The scenarios grouped in the center are either scenarios with relatively small parameter modifications (i.e. scenarios a or b, see tables 3-5), or scenarios involving a change in predation on only a subset of squid prey (i.e. scenarios three, four or five, see table 3-5). On the contrary, scenarios involving an increase in squids' capacity to grow (i.e. increase of maximum growth rate in scenarios 6f to 6j, see table 3-5) stand out from other tests and sit at the opposite end of the axes to the other tests representing a decrease in their voracity (scenarios 2), or a decrease in assimilation efficiency capacity (scenarios 7, see table 3-5), or a decrease in growth capacity (scenarios 6a to 6b, see table 3-5). No particular trend was found regarding the different functional groups on the component axes, due to the many trophic interactions of both species and their dispersed impact on the food web.

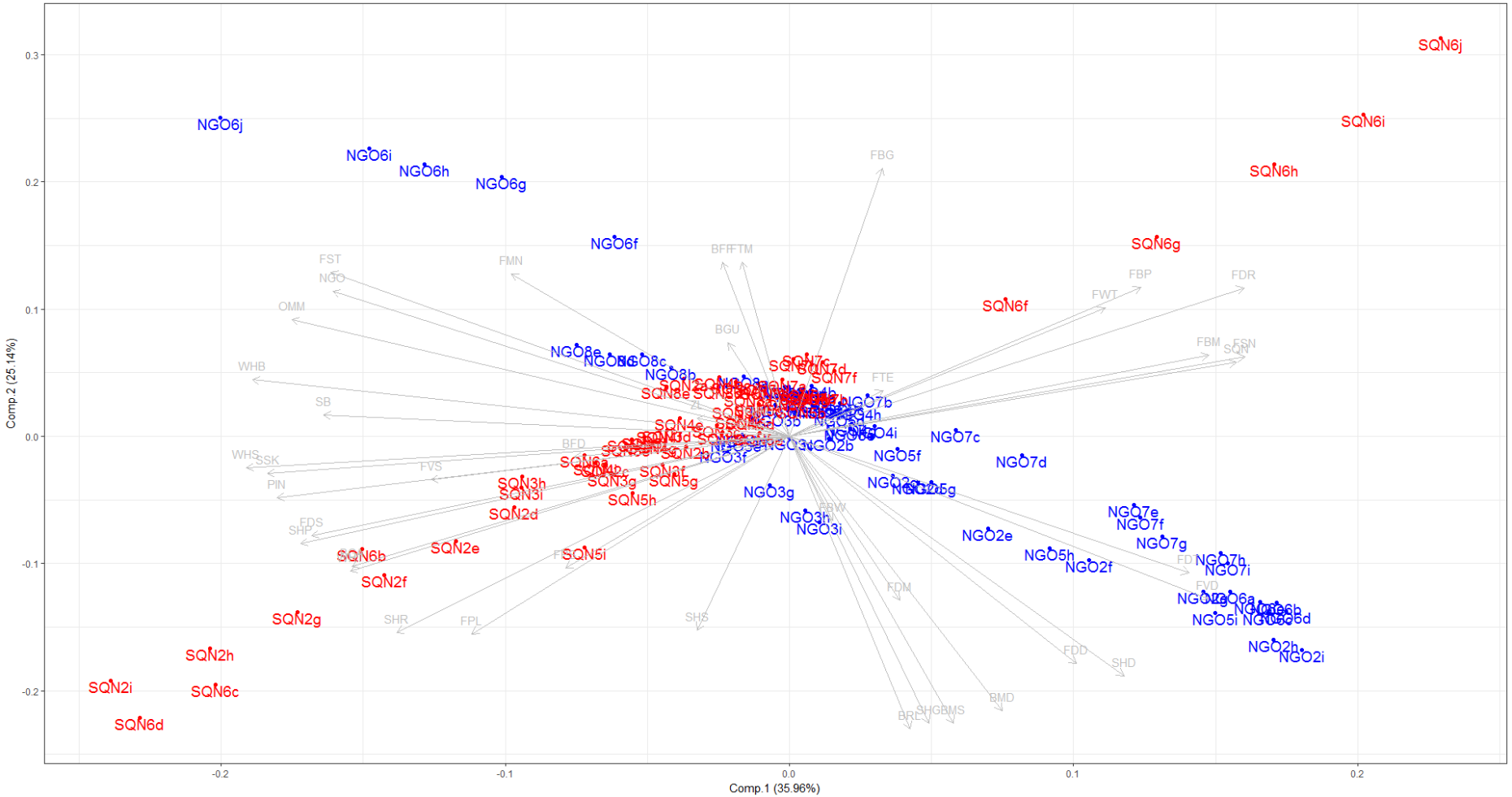


Figure 3-5. PCA results including calamari and arrow squid sensitivity tests.
This PCA figure displays the scenarios along the two axes (Comp. 1 & Comp. 2) where the variability between scenarios is maximized, which is the equivalent of the axis that explains the most variability. In blue are the simulations involving changes to arrow squid parameters, and in red the simulations with changes to calamari parameters. The abbreviations correspond to the functional groups, and associated arrows reflect the effect of the different groups on the component axes and which groups are drawing out scores on those axes. Each scenario's location on these dimensions is based on the relative biomass change across all the groups in the ecosystem.

Biomass trends of arrow squid under the different tests.

When predation is focused on a subset of groups, the result on arrow squid is variable until predation is decreased by more than 50%, after which point biomass steadily declines with the decrease in predation (fig 3-6a; tests 3,4 &5). The decrease in predation on crustacean species has a stronger effect on Arrow squid than our tests on oceanic and neritic fishes. A decrease of 90% in predation on neritic or oceanic fish results in a decrease in Arrow squid biomass of about 14%, while the same decrease in predation on crustaceans results in a decrease in biomass by 90%. Growth of Arrow squid does not show any particular pattern in any of these tests. Instead, the decrease in predation on all those groups together results in a direct reduction in Arrow squid biomass, and growth also drops after predation is decreased by more than 50%. Our test on growth and assimilation shows a stronger impact on Arrow squid biomass than predation tests (fig 3-6b). A reduction in growth capacity of 20% depletes the Arrow squid group by the 40^{th} year, while assimilation requires a 60% drop to have a similar effect. Reducing the growth capacity also affects the size of squids, and a drop of 90% of the growth capacity leads to a size reduction of 73%. The increase in growth capacity shows a very strong effect on the group's biomass, which is more than doubled after a 40% increase on growth. The biomass of arrow squid can be increased by 80% after 40 years when assimilation is maximised, while the size of individuals does not appear to increase.

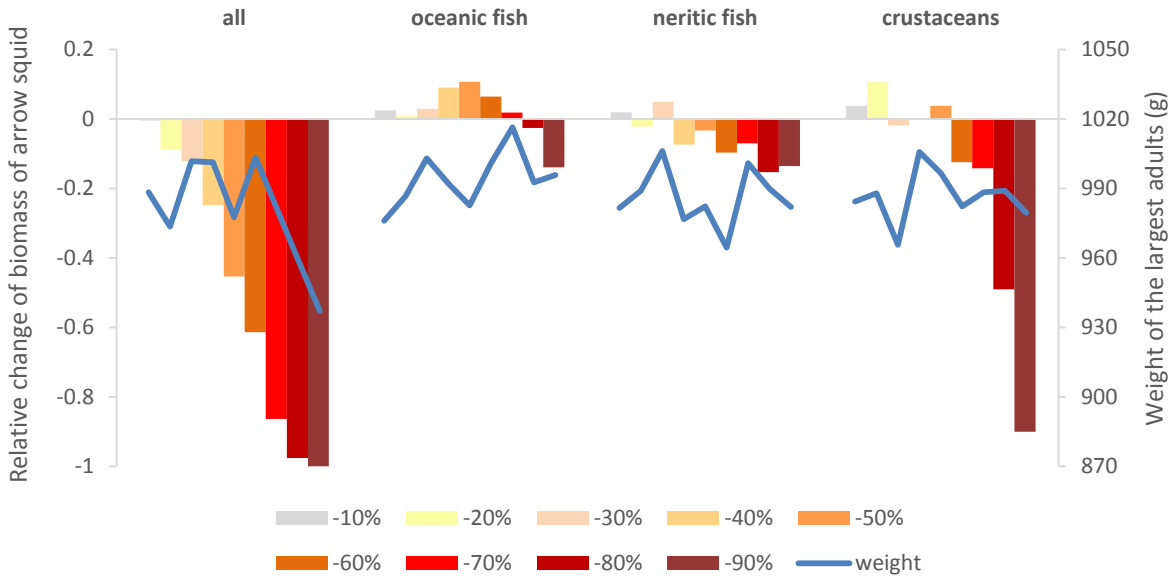


Figure 3-6a. Effect on arrow squid biomass of the changes of predation on various prey groups (tests 2,3,4 & 5).

Each test from a to i decreases the predation voracity by 10%.

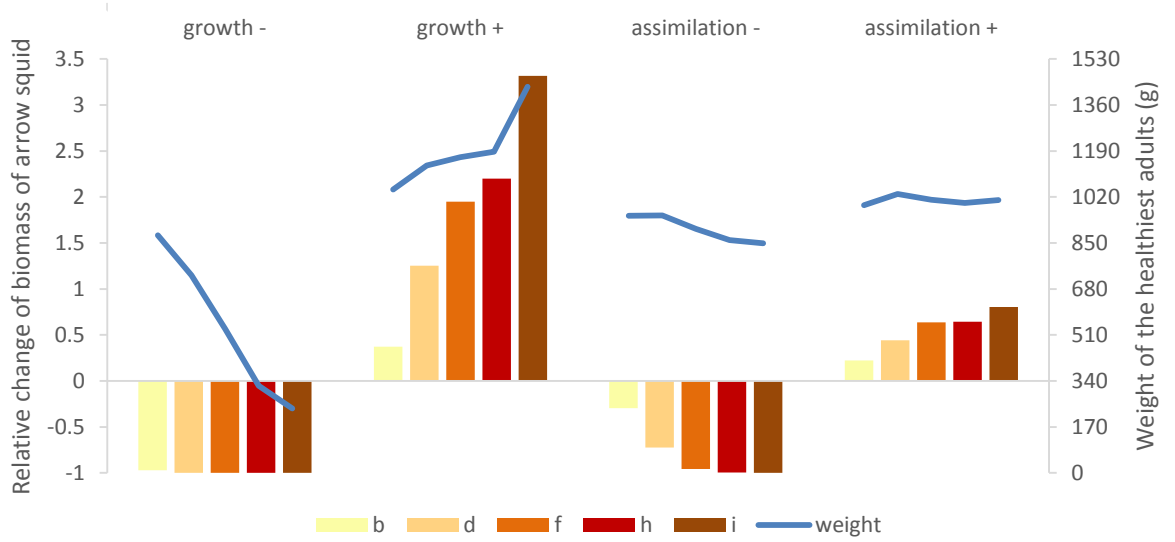
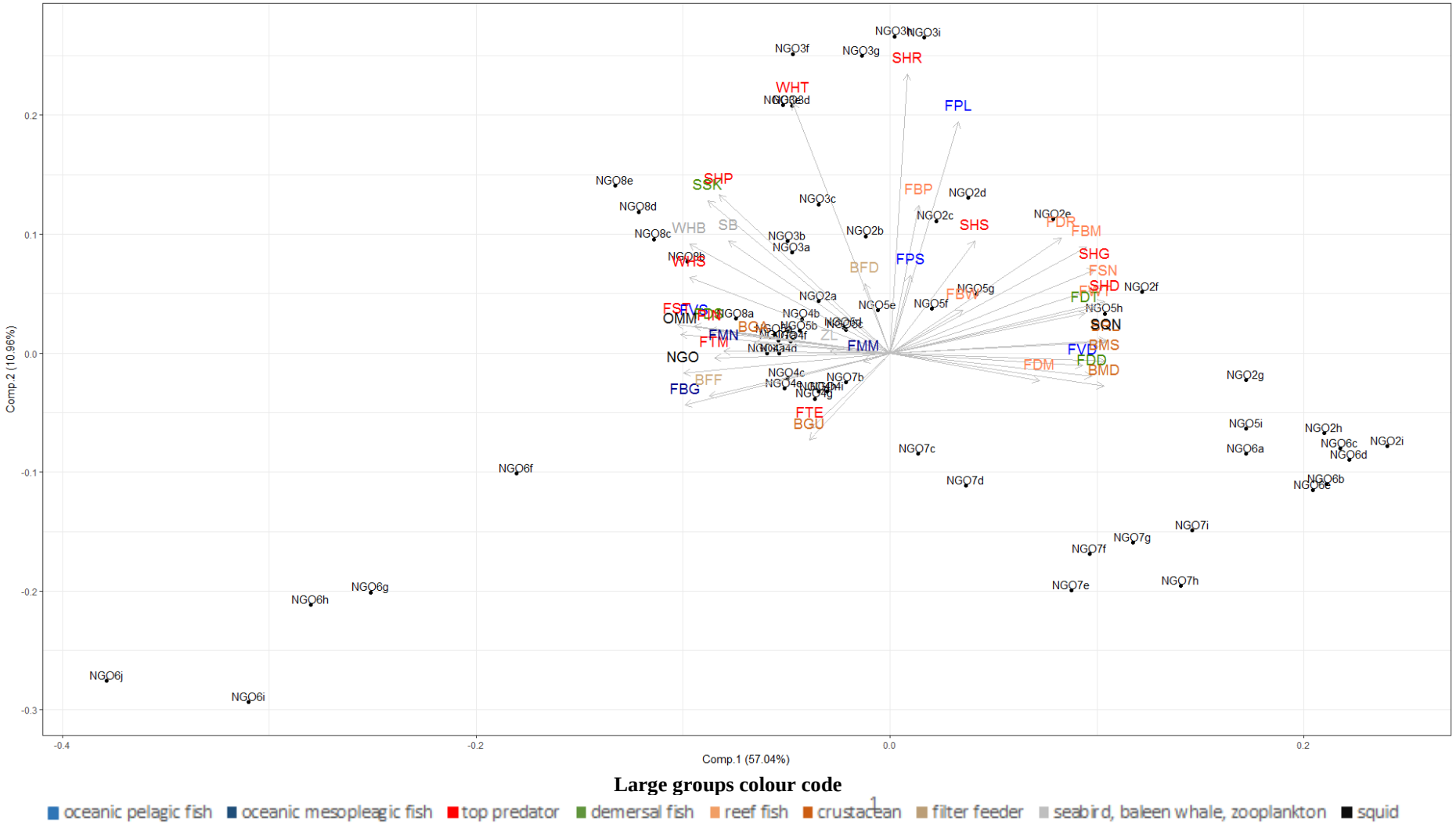


Figure 3-6b. Effect of the change in assimilation efficiency and growth capacity on arrow squid (tests 6, 7 & 8). In this figure, growth is modified by 20% between each category (a to e). The assimilation efficiency is decreased by 10% (assimilation -) and increased by 5% (assimilation +) between each step. These different scales are due to the different window each parameter is limited to by the various processes they affect. I thus used the scales found more appropriate to display the results of the sensitivity tests.

Effect of arrow squid parameter changes on the ecosystem

Tests on the growth parameters of arrow squid clearly stand out from the rest (fig 3-7). As the growth is reduced, scenarios are displayed in more negative values on both axes. Assimilation scenarios are also set apart, and tests with the lowest assimilation efficiencies are relatively high on the Comp.1 axis and low on the Comp.2 axis, while tests with increased assimilation are opposite. Sensitivity tests on predation are more spread on the plot, with tests of reduced predation on oceanic fishes reaching +0.25 on the Comp. 2 axis and tests of reduced predation out on crustaceans reaching +0.17 on Comp.2 axis. Functional groups combined into larger groupings, based on similar habitat and trophic level, do not seem to be gathered together on the plot, indicating that the components of these larger groupings can be impacted very differently by arrow squid.



Large groups colour code

oceanic pelagic fish | oceanic mesopleagic fish | top predator | demersal fish | reef fish | crustacean | filter feeder | seabird, baleen whale, zooplankton | squid

Figure 3-7. Plot of the Principal Component Analysis on all the runs with a modification of a parameter on the arrow squid (NGO group).
The colour of the groups abbreviations are related to large functional categories (i.e. top predators, small oceanic fishes, crustaceans etc…).

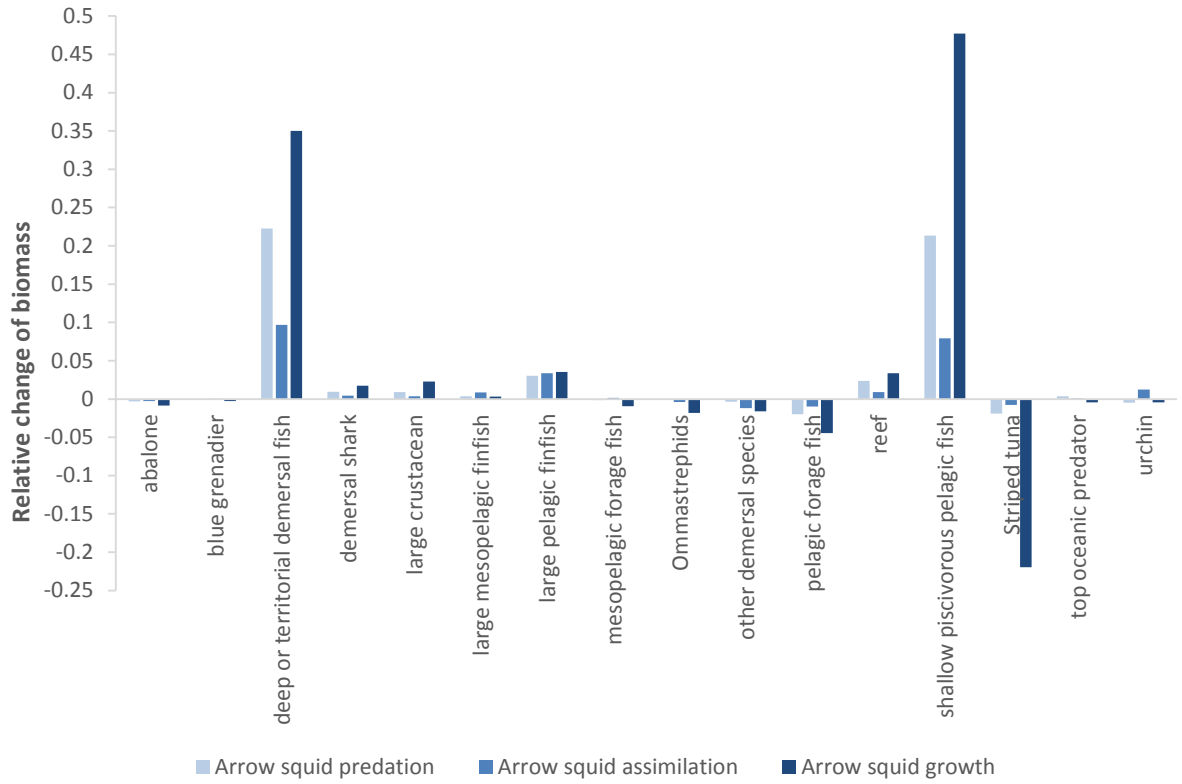


Figure 3-8. Impact of arrow squid on large functional groups of the system.

The predation and assimilation sensitivity were chosen based on the scenarios reducing arrow squid biomass by approximately 25% (scenarios 2d and 7b). The growth sensitivity tests all showed larger changes in results, and for comparability I thus display here the only growth scenario which did not deplete the group before the end of the run (scenario 6a). These biomass changes refer to groups of species with similar results on the PCA (appendix 3-3).

The change in each parameter involved in the feeding or growth of arrow squid leads to a different effect on the biomasses of other groups (fig 3-8). The drop in arrow squid biomass strongly benefits some demersal fish species and shallow piscivorous pelagic fish. It has also a negative effect on forage fishes, and the drop in arrow squid biomass from the reduction in growth also leads to a reduction in the Striped tuna biomass. Direct prey of arrow squid, like pelagic and mesopelagic forage fish (mackerel, sardine, anchovy or myctophids), show a small decrease in biomass, likely due to an increased predation on them from oceanic predators of arrow squid, while large crustaceans (crabs) slightly benefit from reduced predation or growth of arrow squid.

Biomass trends of calamari under the different tests.

The decrease in predation on any group results in a decrease in biomass of calamari of a similar magnitude (fig 3-9a). A reduction of 90% for predation on those groups leads to a biomass decrease of 13 to 17%. These tests also affect the size of calamari, although the size reduction is only about 1% when the predation on one group is dropped by 90%. The reduction of predation on multiple groups together can lead to a drop in calamari biomass of 34%, and a decrease in calamari sizes by about 4%. The tests on growth have the strongest effect on the biomass of calamari (fig 3-9b), with a 20% reduction in growth capacity leading to a drop in biomass of 40%. It also has an effect on calamari size, as a drop in the growth capacity leads to a size reduction of 80%. Assimilation has a smaller but substantial impact on the group's biomass, with a decrease of 20% leading to a decrease in biomass by 15%.

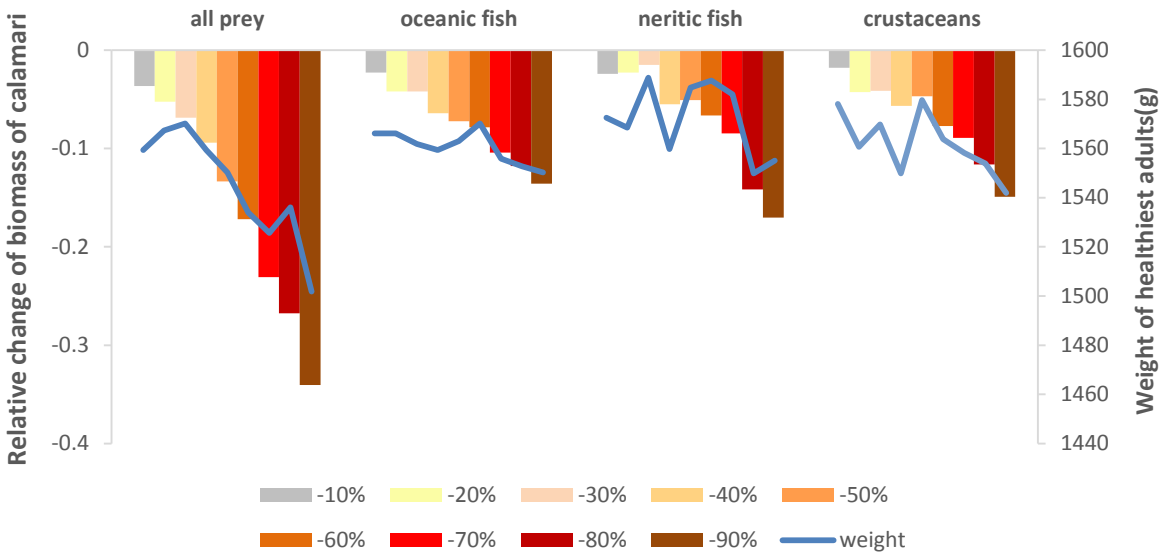


Figure 3-9a. Effect on calamari biomass of the changes of predation on various prey groups (tests 2, 3, 4 & 5).

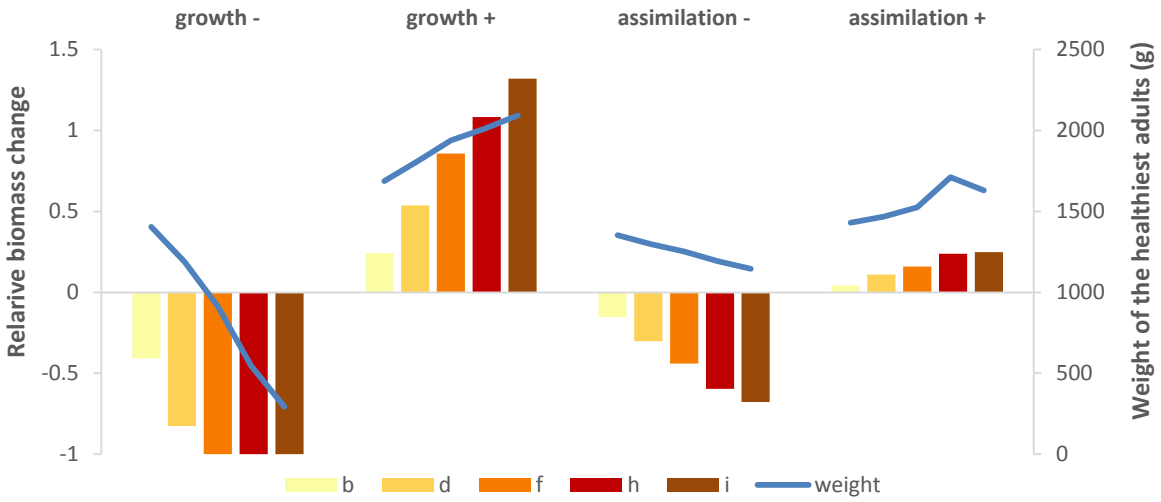


Figure 3-9b. Effect of the change of assimilation efficiency and growth capacity on calamari (tests 6, 7 & 8).

Effect of calamari parameter changes on the ecosystem

The scenarios involving changes on different parameters tend to be displayed in different directions (fig 3-10). Sensitivity tests on decreased growth (SQN3) reached -0.5 on the Comp.1 axis, decreased predation on oceanic fishes reaches +0.5 on the Comp.2 axis and decreased assimilation or reduced predation on all prey reach +0.3 on the Comp.1 axis. Other scenarios appear to be closer to the centre. Many reef associated fish groups (FBM, FSN, FBP and FWT) are gathered together around a (-0.25;+0.3) coordinates, while some crustaceans (BRL, BMD, BMS) are grouped at (+0.7;-0.06).

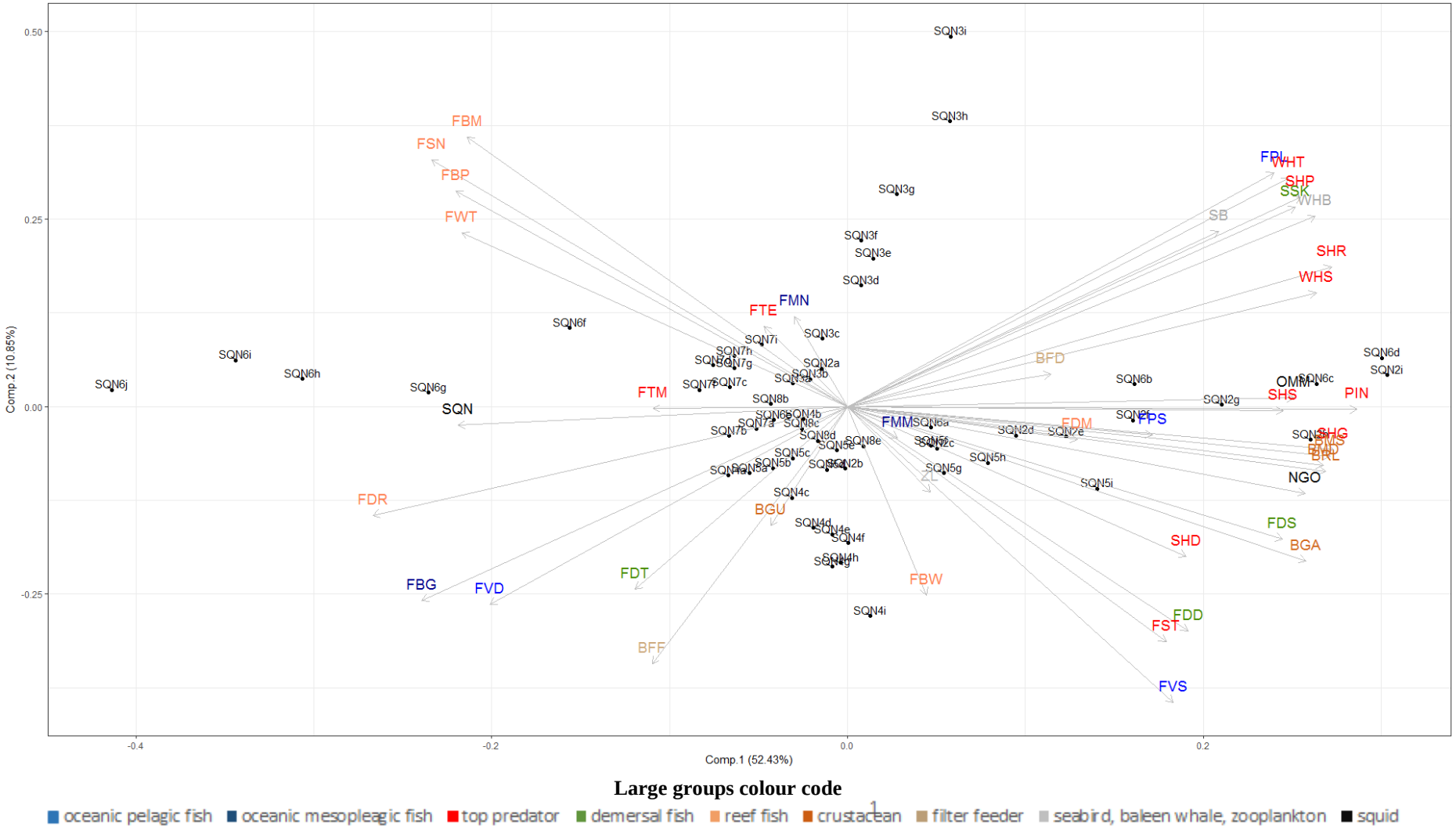


Figure 3-10. Plot of the Principal Component Analysis on all the runs with a modification of a parameter on the calamari (SQN group).
The colour of the groups abbreviations are related to large functional categories (i.e. top predators, small oceanic fishes, crustaceans etc…).

The reduction in calamari growth and feeding parameters affects more neritic species in the demersal groups and reef species, and the oceanic species of shallow piscivorous fish, pelagic forage fish and Striped tuna (fig 3-11). While the biomass of demersal groups is increased, reef associated species are negatively impacted. In the oceanic food web, the changes are detrimental to shallow piscivorous fish, and benefit the pelagic forage fish and Striped tuna. The change in the assimilation parameter often results in a substantially smaller effect, and for some groups has an effect opposed to changes on other groups like reef species, deep demersal fishes and pelagic forage fish. The overall effects of the changes on the food web are relatively small and the strongest changes do not reach 15%.

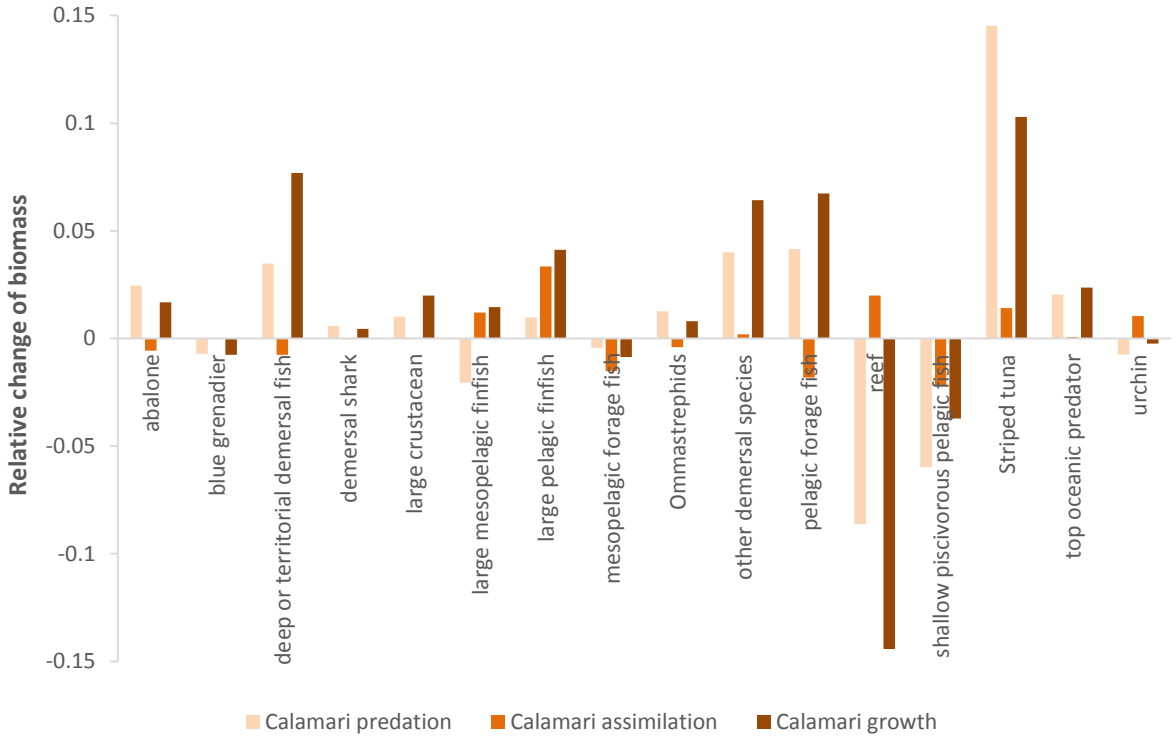


Figure 3-11. Impact of calamari on large functional groups of the system.

The predation and assimilation sensitivity were chosen based on the scenarios reducing arrow squid biomass by 23% (predation scenarios 2g), 30% (assimilation scenario and 7i). The growth sensitivity tests all showed more significant results, and for comparability I thus display here only the growth scenario which did not deplete the group before the end of the run (scenario 6h). Note that the scale of the Y axis is not the same as in figure 3-8 for reading purposes. See appendix 3-4 for comparison.

Discussion

The improvements in the representation of cephalopod ecology in ecosystem models

Our study demonstrates the possibility of representing the ecology of cephalopods in ecosystem models in a more accurate and ecologically relevant manner than previously reported. I successfully represented multiple cohorts per year (fig 3-2a) for our squid groups, included four life stages with exponential growth (fig 3-4), and the capacity to feed on relatively large prey and opportunistic predation (fig 3-3). These traits allowed us to represent the important shift in cephalopod diet (fig 3-3), reflecting observations (Braley et al. 2010; Pethybridge et al. 2012). The relatively low level of cannibalism shown in the figure has been observed at the end of year periods (Pethybridge et al. 2012), which is when our model outputs are extracted. The combination of the exponential growth and opportunism were keys to represent the ontogenic shift in cephalopod ecology and to adequately include them in the food web. Based on the evaluation framework in de la Chesnais et al (chapter II, published), the adequacy of this model to assess the role of cephalopods is significantly improved by our work (Table 3-4). The 'structure' score would go from 3 to 4 (out of a possible 4) and 'data quality' score from 2 to 3; and the overall adequacy of the model to represent cephalopods ecology from III to IV. The improvement of the structure was a key step to allow the use of specific data for the parameterization.

I also show the possibility to use our developments of the Atlantis modelling framework to represent various reproductive dynamics, with several spawning events per year for cephalopod species and a dependence of the cohort abundance on various factors. The reproductive dynamics in our model do not force any variability in the strength of new cohorts, and the seasonal peaks of arrow squid abundance observed are related to the abundance of the secondary producer (fig 3-2b) that is the major food resource for juveniles, and the frequency of spawning events. The delayed response of the biomass of arrow squid to peaks in zooplankton biomass reflects the predator-prey relationship, and

large zooplankton indeed represents about 90% of the amount of juveniles' food intake. The remaining variability of arrow squid biomass is due to other factors influencing the group, including the abundance of secondary prey, the abundance of predator and the temperature. On the other hand, the seasonal peaks of Ommastrephids and calamari biomass have less variability. They reflect the spawning cycle of overlapping cohorts and show less influence of plankton availability. The multiple spawning events per year are critical to represent the dynamic of some cephalopod species. Missing this mechanism prevents us from representing the seasonal variations in squid's populations, and would not allow us to identify the potential adaptive advantage of a year-round reproduction.

Despite valuable insights from treating cephalopods like fish (Pauly 1998) as they have some similar life-history, their differences are too great (O'Dor & Webber 1986) to be disregarded if we want to understand the processes driving ecosystem functioning. This study is, to our knowledge, the first attempt to focus on the exceptional features of cephalopod ecology and how they affect ecosystem functioning. The processes successfully represented in this study should be relatively easy to reproduce on other models around the world where they could be identified.

Processes driving cephalopods dynamics

One of the important results of this work is the substantial difference between the end states produced by modification of arrow squid and calamari parameters as demonstrated in figure 3-5 and appendix 3-4. These results confirm that these functional groups have very different roles in the systems and our initial hypothesis that these groups should be considered as distinctive groups in any modelling exercise. These results would likely be very different for species with stronger habitat overlap and more feeding on cephalopods. The impact of each species on the system would probably be driven largely by its impact on cephalopod species. However, it is very difficult to anticipate the role of such species and the functioning of the associated ecosystem given the potential for nonlinear or indirect effects. This could be the topic of complementary studies and ecosystem models focused on systems that include substantial biomasses of highly cannibalistic pelagic squid.

For both tested squid species, the predation parameter has the smallest effect on the targeted group's biomass while the growth parameter is the most impacting (fig 3-6 & 3-9). Reductions in the growth capacity of both squids very quickly deplete their respective stocks. Although it is difficult to compare the results of each test due to the different scales of associated parameters, the growth tests appear to have the strongest impacts. This is partly due to the size limits put on their predation, as the size of squids decreases, the biomass of available prey is reduced, which causes a negative feedback on growth and predation activity. The specific composition of the squids' diet shows some change (appendix 3-5), but the main change is in the cohorts on which the squids prey, as smaller individuals feed on smaller and younger cohorts. These results point at growth as the key process in the ecological role of the squid species represented, especially for arrow squid, which was the most sensitive to growth tests.

This growth process is even more important in the ecology of the migrating species in comparison to neritic species. The wide spectrum of prey consumed by migrating species allows them to sustain a reduction in voracity on a subset of prey (fig 3-6a), but any growth capacity decline has a strong impact on the group's abundance. Where growth also shows the most significant impact across parameters tested on calamari, its impact on calamari abundance is less than in the arrow squid case. Another difference is that even a small reduction in voracity on a subset of prey is detrimental to calamari (figure 3-9a), before its growth is affected. This is due to the smaller diversity of their predation and being more constrained to the neritic habitat (appendix 3-4a & 3-4b). The effects of all the reductions in growth, assimilation or voracity tested have a lesser impact on its abundance than in arrow squid tests, which is due to the relatively high biomass of the neritic food web (crustaceans and neritic fishes) where food resources are more available. These results reflect an ecological strategy difference between migrating squids, investing in movements and opportunism to support their fast-growth, and some more neritic species whose growth is supported by the abundance of some prey groups in the neritic area.

Impact of local squid species on the South East Australian model

The population dynamics of arrow squid shows our capacity to represent the sensitivity of cephalopod abundance to primary or secondary production (Nishikawa et al. 2014). The high abundance of arrow squid in autumn-winter in the results of the model (fig 3-2a) has been observed in South East Australia (Jackson et al. 2005; Stark 2008), and our model suggests that secondary production could be the best explanatory variable for arrow squid variability (Stark et al. 2005). While the dynamics of local oceanic ommastrephids other than the arrow squid are relatively poorly known, the abundance of calamari is believed to be strongly tied to the temperature encountered during the growth of cohorts (Pecl & Moltschaniwskyj 2006). These differences are a key feature of the model as the different sensitivity of cephalopod species to external factors has been observed in South East Australia. Arrow squid growth is often stronger in the colder and richer water (Stark 2008) while temperature seems to play a stronger role on the growth capacity of calamari, which grows faster in warmer waters (Pecl & Moltschaniwskyj 2006; Triantafillos 2002) and abundance (Steer et al. 2007).

The numerous trophic links of arrow squid is reflected by the impact on groups from very different habitats; demersal, pelagic or neritic (fig 3-8). We could use the PCA results (appendix 3-3) to gather functional groups into smaller and more relevant aggregated groups than was done in figures 3-7 and 3-10. Such aggregation allowed me to present results in a clearer manner based on species impacted in a similar way by the tests – e.g. based on common traits, mainly habitats and diets. The simulations decreasing the group feeding and growth capacity result in a strong positive impact on shallow piscivorous pelagic fish (Snoek, Australian salmon), a group linking the neritic and oceanic food webs that is competitor and prey of arrow squid. The outcomes of the changes also have a strong positive impact on deep demersal fishes. This is due to the predation of arrow squid on some juveniles (the youngest cohorts) of these species that spend early life in arrow squid habitat, although this may be over-estimated by the model. Despite the reduced predation from the squid group on pelagic forage fish and on mesopelagic forage fish, these groups are negatively impacted by the modifications of the parameters. As the abundance of arrow squid is decreased, some top oceanic predator feeding

substantially on this species in the base model (i.e. arrow squid represents 5%, 3% and 22% of the diet of pinnipeds, dolphins, and mesopelagic predators like swordfish in the base model) increase their predation on forage fish groups that represent an alternative food resource (i.e. pelagic forage fish part in the diets of pinnipeds, dolphins and mesopelagic predators is increased by respectively 5%, 2% and 10%). The very high biomass of these forage groups also acts as a buffer for the oceanic predators, which explains the relatively small impact of our changes on most oceanic top predators and large finfishes. It also explains the stability of arrow squid size when its assimilation is increased. Due to the relative abundance of prey, this higher assimilation results in a lower consumption by arrow squid individuals and favours the increased abundance. The substantial positive impact of the parameter changes on striped tuna is due to their specialization for arrow squid as prey (arrow squid represents 40% of their diet) in our model, or low opportunism, which causes the depletion of arrow squid to be more detrimental for them than for other large predators. In the neritic food web, the small relative change of biomass in crustaceans in calamari tests (figure 3-11) corresponds to a substantial change of absolute biomass due to the high abundance of these functional groups. The increase of their biomass benefits the demersal and reef species that feed on them.

In comparison, the response of the different functional groups to calamari sensitivity tests is more dependent on their habitats than in the arrow squid tests (fig 3-7 and fig 3-10, appendix 3-4). The decrease of abundance of calamari is relatively constrained to neritic groups like reef or demersal fishes (fig 3-8 & 3-11). As the biomass of neritic groups are substantially higher in the model compared to pelagic groups, the small relative changes of groups like crustaceans and various demersal groups still reflect large biomass changes However, this neritic squid species still has an impact on some oceanic groups, including pelagic forage fishes and subsequently pelagic predators like finfishes. This is probably partly due to a relatively wide distribution of our calamari group that probably spreads away from the coastlines more the calamari do in reality. This suggests that if prey is available for calamari in these areas, their abundance is more limited by biological traits underestimated in our model. It could be linked to depth or temperature limitations. The strong effect of calamari on Striped tunas probably results from this bias, as they benefit from the increase in the

demersal food web associated with the reduction in calamari that represents a significant part of their diet.

Our results support findings of Bulman (Bulman et al. 2011) and Johnson et al. (Johnson et al. 2013). These earlier ecosystem models show arrow squid having a substantial impact in food webs, although mesopelagic forage fish in these models have a stronger effect on similar groups (Johnson et al. 2013). Our model also shows the important role of calamari in the neritic food web, which support the model made by Watson et al. 2013. However, the results of their model point to a relatively small impact of arrow squid. This difference in results is likely due to the neritic focus of their model, and an associated under-evaluation of the oceanic food web and potentially the species linking the two habitats.

The high variability in cephalopod recruitments is strongly due to their population structure. There is a major turn-over of the population after each spawning event (Boyle & Boletzky 1996; Rodhouse et al. 1998), and the survivability of each cohort is determined by various factors. Our new features added to the model allowed us to represent more accurately the different modalities of turnover between species. The quantitative effects of those biotic and abiotic factors are still partly uncertain today, and a more precise observation of squid responses to them could allow us to improve the quantitative accuracy of the model. However, their effects are well represented here compared to other models, as the seasonal dynamics of each species correspond to the observations that have been gathered so far on the relative strength of these factors for each species. The sensitivity of squid to particular factors driving cohorts' success, like food availability or abiotic factors, were successfully represented, although more field observations are probably required to improve the model accuracy and predictive power. In addition, this study points to the various key processes driving cephalopods ecology, highlighting the importance of various processes in the squids' life history. While growth capacity and associated voracity are key processes for arrow squid species migrating between habitats and whose life history seems focused on a growth race, the more neritic calamari is less sensitive to its feeding capacity and abiotic factors will have a relatively stronger influence on their dynamics.

Model limitations

In order to represent a system as close to observations as possible, models are often calibrated to fit fisheries catches or abundance surveys. This increases the accuracy and relevance of models. However, local cephalopod fisheries are too spatially and temporally localised, with relatively low catch (apart from the depleted cuttlefish of the Spencer and St Vincent Gulf) to allow a relevant "fitting". Our model is thus based on the SEA region and represents the local ecological system the best, but should be used with caution to quantify the impact of cephalopods in the food web. A more extensive data set would be needed to have the best information on cephalopod abundance and location and allow us to represent the South East Australian ecosystem accurately. Nonetheless, as a function of our improvements to the ecological processes of cephalopods in the model, I could already draw valuable insights on the role of local cephalopod species on the food webs and on the key processes involved.

Another difficulty faced was the accurate representation of the growth of cephalopods and its correlation with their diet. Due to the dependence of food availability with predator size, our model represents the key diet shift between juveniles and adults (fig 3-3). However, the similarity of the diet between the two adult stages is probably overestimated. This is likely due to the fact that the size selection is roughly represented and strongly depends on maximum and minimum prey sizes. Different adult squid stages thus keep preying on similar prey groups, and feed on prey stages and cohorts of increasing size as they grow. A more accurate prey selection could point at an eventual shift of specific predation between adult stages. Our model, however, does capture the key ontogenetic shift of predation as squid reach the capacity to feed on fish and crustacean species after feeding on primary and secondary producers.

The model probably underrepresents the variability in abundance of calamari cohorts (Steer et al. 2007). This is due to the relatively stable temperature trend in the oceanographic conditions of our

model that repeats 5 years of observations in a continuous cycle. A model applying more constraining abiotic features could provide better insights on the dynamics involved and the impact on the ecosystem. On the other hand, long-term sampling of the abundance of arrow squid in the region would allow us to validate their dependence on secondary producers and identify any over-estimation or under-estimation by the model.

The representation of different octopus groups in the model was not successful, as the model could not reach a stable abundance. The low abundance of octopus species compared to many other groups of the neritic food web prevented us from having a group able to durably sustain predation from local predatory groups like pinnipeds, toothed whales or demersal sharks. Calibrating those octopus groups adequately would require additional focus on these groups and their trophic links or abundance. It may also require representation of specific sub-grid scale processes that would allow for coexistence without self simplification of the model (which can occur if model processes do not specifically distinguish groups and their niches) (Fulton 2001).

A related issue that was faced is the balance between the neritic and the oceanic food webs. The relatively low sensitivity of calamari to our tests coupled with the substantial response from some pelagic groups may be due to the complex representation of the neritic food web compared to the oceanic food web in the model. This gives calamari the possibility to feed on a bigger number of specific groups while the oceanic squids are feeding on more generalist groups (i.e. small planktivorous fish, large planktivorous fish, and migratory mesopelagic fish). In the relation between oceanic and neritic foodwebs, the impact of arrow squid on some demersal groups also might be partly overestimated. These prey appear to acquire more importance in the squid's diet (appendix 3-5) than observed in local studies (Braley et al. 2010; Pethybridge et al. 2012). This could indicate either a reduction of the activity of arrow squid at daytime when they are in deep water, or a low voracity towards the demersal species that exceptionally do not fit the high opportunism of squids as we implemented here. Both these hypotheses could explain the relative low catches observed during the day by fishers (Green 2011).

Our model highlights the importance of growth for arrow squid as their ability to feed and reproduce are strongly conditioned by it. This particular feature could be true for many voracious migrating squid species around the world (Rodhouse & Nigmatullin 1996; Jackson et al. 2003). Their dispersed impact on the food web is thus likely to also be a recurrent trait across the globe. Updating models in several regions harbouring these species could provide a significant confirmation or rebuttal for this hypothesis. This would require a significant amount of work, both in terms of modelling adaptations, and in terms of data collection. However, the substantial impact of these species on the system highlights this necessity.

It is a key challenge today to put some focus on the role of cephalopods in marine systems as these ectotherm species are highly sensitive to upcoming environmental changes (Angilletta et al. 2002; Rodhouse et al. 2014), and their habitats and the distribution of their preferred abiotic conditions are changing at a fast rate today (Pierce et al. 2008; Rodhouse 2010). Migrating species, which are already facing a large range of environmental conditions due to their migrations, could still be significantly impacted. The temperature is indeed recognized to have a significant impact on the growth of squid species, generally increasing their growth as temperature goes up (Forsythe 2004), which would cause key changes and shifts in their ecology and their role in marine systems. The effect of temperature is also very likely to affect planktonic producers, increasing the productivity and abundance of a key resource for the growth of juveniles and the renewal of stocks (Nishikawa et al. 2014). The effects of these combined processes on squid species could thus cause critical changes on their ecology. As for more neritic and habitat constrained species, their life-history puts them in relatively similar abiotic conditions thorough their life, but upcoming changes will place them in new conditions and could very well provoke major changes in their ecology. Temperature has been shown in general to critically increasing their growth rate capacity as long squids are within their environmental niche (Domingues et al. 2006; Jackson & Moltschaniwskyj 2002; Pecl 2004; Pecl & Jackson 2008). Representing the mechanisms driving the response of cephalopod to changing

environmental conditions could give us very valuable insight on the potential ecological shifts undergone by these species and what modifications they could drive in the system.

Our results show that the two squid species have relatively low impacts on predator groups of higher trophic levels except from the more specialised predator groups. Their impact on food web is mitigated by the relatively large biomass of their prey groups like crustaceans or forage fishes. Although this could point to an opportunity for fisheries to exploit a new resource, these results should be carefully handled. The effect of oceanic squid on a few groups is still substantial. Moreover, this is only the first assessment (to our knowledge) of their impact of the food web taking in to consideration the complexity of their ecology and results therefore suffer several limitations mentioned previously. Nonetheless, while climate rapidly changes environmental conditions, an increased interest from seafood markets and fisheries in the last decades is already subjecting squid stocks to increasing pressure. Their responses to abiotic changes will thus be combined with a reaction to fisheries pressure. This combination could very well cause critical changes in cephalopod ecology and result in substantial changes in the functioning of marine ecosystem and in the services they provide to our societies. It is necessary for us today to analyse the effects of these changes on squid's ecology and their impacts on systems functioning. This is an important and urgent step to improve our understanding of ecosystems changes and provide appropriate foresight for management.

Chapter 4 Effects of climate change on ecosystem functioning and on the role of cephalopods.

Abstract

Marine ecosystems are subjected to powerful external pressures today, most notably increasing temperatures. These environmental forces are already leading to changes in species ecology, and therefore in the general functioning of ecosystems. From this perspective, the rapid life-cycle of cephalopods and their strong sensitivity to environmental factors has been associated with a rapid response to temperature changes. Their early responses will affect food webs and may drive changes in ecosystems functioning. This chapter aims to assess the impact of climate change on species life-history traits, and on the resulting changes in ecosystem functioning, with a particular focus on the changes related to cephalopod ecology. I focus on the increase in temperatures as the most impacting factor, and on the South East Australian region, a recognized hotspot of global warming. According to our model, the strong increase of temperature over 50 years following the RCP8.5 scenario is beneficial to arrow squid and calamari species as their biomass increases by up to 15% at the end of the scenario. They respond quickly to changes in producer abundances, and exert a competitive and top-down control on forage fishes. This change at the middle trophic level in this wasp waist structured system results in a general decrease of biomass of upper trophic levels.

Introduction

Oceanic systems, especially along the coasts, are currently undergoing critical changes under climate change, affecting food web dynamics, species distributions (Pecl et al. 2017) and productivity (Doney et al. 2012; Harley et al. 2006; Hoegh-Guldberg & Bruno 2010). The South East Australian region has been identified as an ocean warming hot-spot, with local ecosystems undergoing associated rapid changes (Hobday & Pecl 2014; Wu et al. 2012). Improving the knowledge of interactions between the components of an ecosystem and combined pressures is thus necessary to provide valuable insights for the management of human exploitation activities. In this regard, integrative approaches and ecosystem models have proved to be powerful tools to assess the impacts of stressors on systems functioning and explore potential system responses (Coll et al. 2008; Fulton & Gorton 2014; Marzloff & Melbourne-thomas 2017). To this end, understanding the ecological changes of the key drivers of ecosystem functioning is essential to anticipate their dynamics and transformations (Palumbi et al. 2009). Many ecological traits point to the cephalopod taxa as a key group in ecosystem functioning (Boyle & Rodhouse 2005; Rodhouse & Nigmatullin 1996; Smale 1996; Young et al. 2013; chapter II) which is evident as well in ecosystem models of South East Australia (chapter II and III). Cephalopods are believed to have a central role in food webs, as they are voracious predators of many low and mid trophic level groups (Rodhouse & Nigmatullin 1996). Combined with their fast growth rates and high productivity (Rodhouse & Nigmatullin 1996; Jackson et al. 2003; Jackson & Pecl 2003), their central ecological role - as an important predator on the one hand and an important source of food for many top predators on the other (Boyle & Rodhouse 2005; Cox et al. 2002; Field et al. 2013; Griffiths et al. 2010; Olson & Watters 2003; Smale 1996) – makes cephalopods important agents of change.

In this context of strong pressure from climate change and human exploitation, understanding the influence of cephalopods on ecosystems functioning is likely to be paramount, given their sensitivity to environmental change (Dupavillon & Gillanders 2009; Pecl et al. 2014; Rodhouse et al. 2014), fisheries (Boyle & Rodhouse 2005), and their responsiveness to fisheries and ecological changes (Pecl

& Jackson 2008; Robin & Denis 1999; Rodhouse et al. 2014). Cephalopods indeed have a strong potential to adapt to external pressures due to their short life-cycle and fast turn-over rate (Lee 2002) and their opportunistic behaviour (Rodhouse 2001; Rodhouse 2008). This adaptive capacity may be partially or largely behind why cephalopod abundance is increasing worldwide (Doubleday et al. 2016), as they appear to quickly fill ecological niches left vacant by overexploited finfish stocks (Caddy & Rodhouse 1998; Pecl & Jackson 2008). Simultaneously, we see a cultural rise of interest from consumers (Vidal et al. 2014) and often from recreational fishers (Mobsby & Koduah 2017), and an economic opportunism from many fisheries, which see cephalopods as an alternative to depleted finfish stocks (Doubleday et al. 2016).

Despite a significant body of work on cephalopod ecology and their sensitivity to environmental conditions (André et al. 2010; Pierce et al. 2008; Robin et al. 2014; Rodhouse 2010), cephalopods are often poorly represented within ecosystem models (chapter II). Most model considerations to date have relied on simple biomass representations, but these simulations have provided limited benefits so far in terms of improving our understanding of the dynamic nature of the role of cephalopods in ecosystem functioning. The study conducted here aims to provide insight on the potential role of cephalopods to drive ecosystem changes under climate change, by using a well elaborated model and exploring its responses to scenarios with climate signatures.

Material & Methods

The ecosystem model of the South East Australia region built with the Atlantis framework and with a strong focus on cephalopods ecology was used (chapter III). The scenarios of climate change explored with the model are based on CMIP 5 climate projections and various scenarios pertaining to the intensity of exploitation by cephalopod fisheries.

Atlantis modelling framework

Atlantis is a deterministic end-to-end ecosystem model (Fulton et al. 2007; Fulton 2011; Fulton & Link 2014) that attempts to represent each of the key components of an ecosystem, fitting together physical, biological and socio-economic processes dynamically. Models are spatially resolved in three dimensions, divided into horizontal boxes and vertical layers. Biogeophysical and ecological process representations direct and control the flow of nutrients through the spatial seascape of the model, as well as the food web functional groups and human exploitation components of the modelled system. This degree of resolution allowed us to represent the effect of climate change on oceanographic conditions and on ecological processes affecting the functional groups of the food web.

The South East Australian Atlantis model

Our model was based on the previously published SE Australian model (Johnson et al. 2013), but updated to version 2 of the Atlantis code – which includes new cephalopod process representation. The functional group representation in the model was expanded so that it makes the distinction between various cephalopods groups with different ecological traits, caught by different fisheries, or with observed sensitivity to climate environmental changes (chapter III, table 4-1). Given their biomass in the system and their fisheries importance, this study focuses on the role of the three squid groups in the model.

Table 4-1: Cephalopod groups of the South East Australian model and related catches/fisheries.

Group (*species*)	**Group particularity**
Arrow squid (*Nototodarus gouldi*)	Commercial & recreational fisheries' target
Oceanic squids (*Ommastrephes bartramii and Todarodes filippovae and others*)	Potential new fisheries resources
Calamari (*Sepioteuthis australis*)	Commercial & recreational fisheries target
Giant cuttlefish (*Sepia apama*)	Depleted stock
Pale octopus (*Octopus pallidus*)	Commercial fisheries target
Gloomy octopus (*Octopus tetricus*)	Range shifting species & potential fisheries target

Representing the effect of climate change on species physiology

The effect of environmental changes on all the modelled groups is represented through the metabolic dependence of several processes on the environmental conditions, particularly temperature (table 4-3).

Studies of the sensitivity of cephalopods to changes in pH (Birke et al. 2018) or salinity (Bazzino et al. 2005) were scarce and too uncertain to allow for a reliable parameterization of these influences in the Atlantis model; representing the effects of these drivers in detail would be highly speculative. Thus, the influence of ocean acidification and salinity in the model was restricted to defining preferred (or tolerated) windows for these properties, beyond which the cephalopods moved away (potentially completely out of the system if no suitable conditions could be found).

In contrast, the effect of temperature has been well researched and is considered to be predominant driver for many species of cephalopod (Forsythe 2004; Moltschaniwskyj 2004; Pierce et al. 2008) and fish (Elsdon & Gillanders 2002; Pauly 1980). Cephalopod species have been identified to be particularly sensitive to temperature, and temperature effects on species of South East Australia are well documented (Green 2011; Moltschaniwskyj 2004; Payne et al. 2011; Pecl 2004). This work was thus focused on the realistic representation of temperature changes on cephalopods in South East Australia and on the sensitivity of ecological processes to temperature (fig 4-2). Many processes are restricted to a favorable temperature range, constraining the survivability of groups. Within this range, processes are further regulated by a scaling function related to temperature (fig 4-2).

Table 4-2: Ecological processes affected by environmental context.

Processes	Note	Environmental effect
Feeding	Volume of water searched for food by individuals each day.	Scaled
Growth	Growth rate of an individual in ideal environment (temperature, food etc…)	Scaled
Background natural mortality	Quadratic mortality (density-dependence)	Scaled
	Linear mortality	Scaled
Spawning		Environmental window only

Note: "scaled" refers to the use of a scaling function on the parameter (fig 4-1).

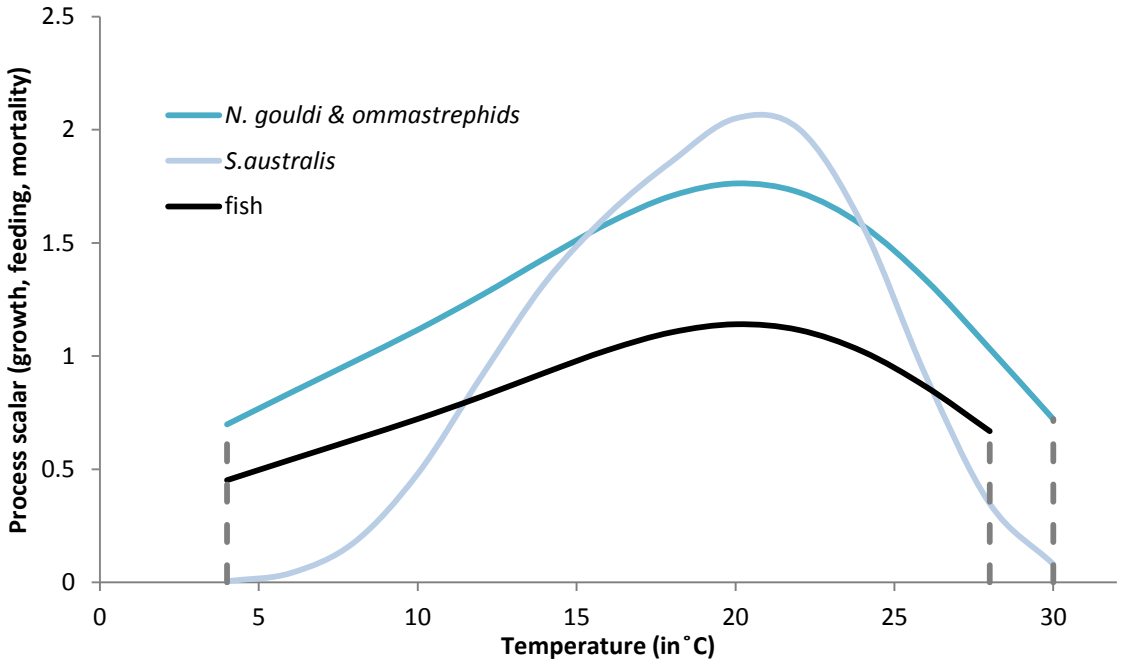


Figure 4-1: Environmental niche and habitat preference. Effect of temperature on growth of two squid groups, with a generic finfish scalar provided for comparative purposes.

The aim of these specific scalars is to simulate the various physiological responses of each group to environmental changes. Figure 1 displays the temperature scalar of *S. australis* and the other Ommastrephids group. While the growth of Ommastrephids has been observed to depend on food availability more than on temperature (Bower & Ichii 2005; Stark 2008), the growth of *S. australis* is more sensitive to temperature (Pecl & Moltschaniwskyj 2006; Triantafillos 2002). The scalar parameter of *S. australis* is thus strongly related to temperature compared to the scalar of Ommastrephids. When possible, the temperature dependence of each species in the model was taken from studies focused on environmental sensitivity (Appendix 4-1 and 4-2). However, this type of study was too scarce for many groups. The temperature limits of most groups were thus taken from observed temperature range in their habitat and the optimum temperature from the conditions where the group was found the most abundant.

Climate change in the oceanographic model

The temperature data from the oceanographic OFAM (Ocean Forecasting Australian Model) model (Oke et al. 2013) provided the environmental conditions for the runs. Rather than risk introducing a bias or oceanographic artefact in switching from historical to future state forcing files an anomaly approach was taken to representing temperature – with the anomaly extracted from the OFAM model run under the climate (fig 4-2) applied to the historical forcing files to produce the realised change. The influence of the change was handled differentially with depth as reflected by the OFAM output. Future scenario explorations using the ecosystem models would benefit from using a complete set of drivers from the climate projection model. This was not possible as yet due to the fine resolution of physical processes needed on the shelf versus what was possible in the OFAM output using existing output as it led to a bias in driver state versus historical observations which undermined computational integrity. Revised versions of the global and downscaled physical models are anticipated to remove this issue in the future.

The standard simulation is run without long-time trends in physical drivers, simply continuously repeating the environmental conditions of the first 5 years. The second simulation uses the RCP8.5 scenario (Vuuren et al. 2011), which assumes a fast increase of temperature (fig 4-2) as a result of high human population growth and moderate technological changes, leading to high energy demands and GHG emissions (Riahi et al. 2011; van Vuuren et al. 2011). This particular scenario was selected because (i) a regionally downscaled version is available for use with Atlantis; (ii) there is little divergence between the various climate scenarios over the short term (the period managers and industry most care about for their planning) due to committed warming; and (iii) the scenario can be used as an upper bound on future change and so can be used as a reference set for identifying the potential effect of climate changes on the food web. Despite the availability of 100 year forecasts, we ran scenarios only over a 50 year time frame, as this was considered sufficiently long to provide useful insights, and longer scenarios (i) increase uncertainties in terms of the final results and (due to the omission of processes acting on those longer time frames) (ii) greatly increase run time for the simulations.

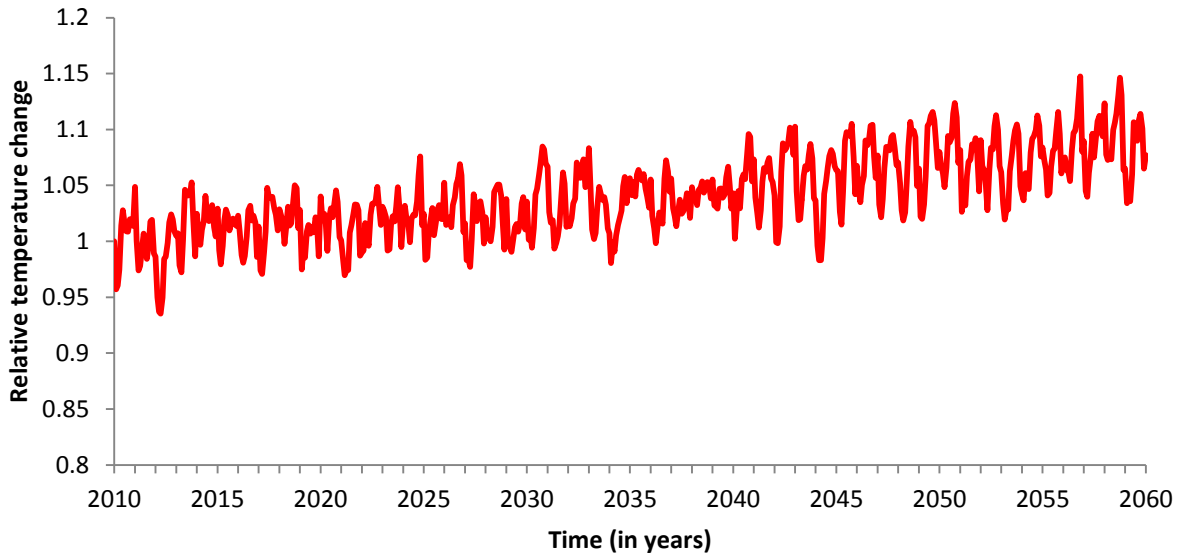


Figure 4-2: Average anomaly for sea surface temperature (SST) over the model area following the IPCC scenario 8.5.

This shows the change in temperature compared to the value at the start of the model (January 2010).

Results

The increase of temperature – of about 1.4°C (ranging from a 1.75°C increase in the warmest to 0.9°C in the coldest one) – causes biomass changes throughout the foodweb (appendixes 4-3, 4-4 & 4-5), although there is a good deal of heterogeneity across groups. The biomass changes of primary producers do not appear to follow a particular linear trend; for example, the biomass of zooplankton groups is decreased for the first 15 to 25 years, before they recover partially or reach a biomass superior to the standard scenario. Algal groups have an exponential increase of biomass as the temperature is increased. In the oceanic food web most vertebrate groups reach the end of the run with a substantial decrease of biomass (appendix 4-5). Crustaceans also appear to generally have a decrease in biomass. In the neritic vertebrates, most groups also suffer a decrease in biomass, but responses are more variable and some groups, such as warehous and trevallas, shallow territorial fishes or gummy sharks, benefit from the climate change scenario. Overall, however, most groups (36 out of 55) are still within ±20% of the base scenario biomass.

The squid species represented in this model have very different responses to the temperature changes (fig 4-3). While arrow squid's biomass substantially decreases (down by 55%) for the first 20 years of temperature increase, it then recovers, until after 35 years it rises above the biomasses seen in the base scenario during the same period, stabilizing at about +15% after 45 years. The generic ommastrephid group shows a similar trend, though with less variation, initially dropping by about 10% before making a recovery and stabilizing at about 1.5% below the baseline levels. The dynamics of these two species follow the dynamics of the secondary producers that are the main prey of juveniles. Neritic squid biomass varies by ±6% for the first 20 years of temperature increase and then rises to about +10% until the end of the run.

In general, trends in the biomasses of cephalopod predators follow those of their squid prey; oceanic top-predators (Pinnipeds, pelagic sharks) follow the biomass trends of oceanic squids, but the response amongst the demersal predators' is more variable. The predators of arrow squid initially decrease - pelagic sharks by of 10% and striped tuna by 30% - before partially recovering – pelagic sharks ending up only 5% below baseline conditions and striped tuna 10% below. The main predators of ommastrephid groups, two pelagic top predators, pelagic sharks and tunas, have a biomass trend very similar to the ommastrephid abundance.

The abundances of arrow squid oceanic prey show the same trend as arrow squid, though with a smaller change in amplitude (fig 4-4). In contrast, the rise of temperature causes an increase in biomass of demersal fish, species with various trophic relationships with neritic or migrating squid, for the first 35 years, before their abundance decreases, ultimately reaching a level 9% below the biomasses in the baseline scenario. The oceanic pelagic prey of ommastrephid squid follow similar trends to each other but with various amplitudes (fig 4-5). They initially decrease, over the first 35 years, and then partially or completely catch up with the biomass of the standard scenario. While zooplankton abundance shows relatively little variability (minimum -6.5%) and rises above the baseline scenario biomass, the other prey, mesopelagic fish and large pelagic planktivorous fish have their abundance drop by -50% and -7% respectively, before stabilize between 10% and 13% below

the levels of the baseline scenario. Prey of neritic squids follow very different trends, although overall the degree of variation shown is smaller than for prey of other squid groups (fig 4-6). Nektonic prey, specifically prawns and large zooplankton, have their biomass increase by 2-6%, while the abundance of other crustacean prey continually decreases as the temperatures increase. Amongst the finfish, while the snapper group shows declines in the climate change scenario (biomass down by about 20%), the biomass of demersal fishes actually marginally increases above the levels of the baseline scenario after 37 years - stabilizing at about 2% above baseline biomasses.

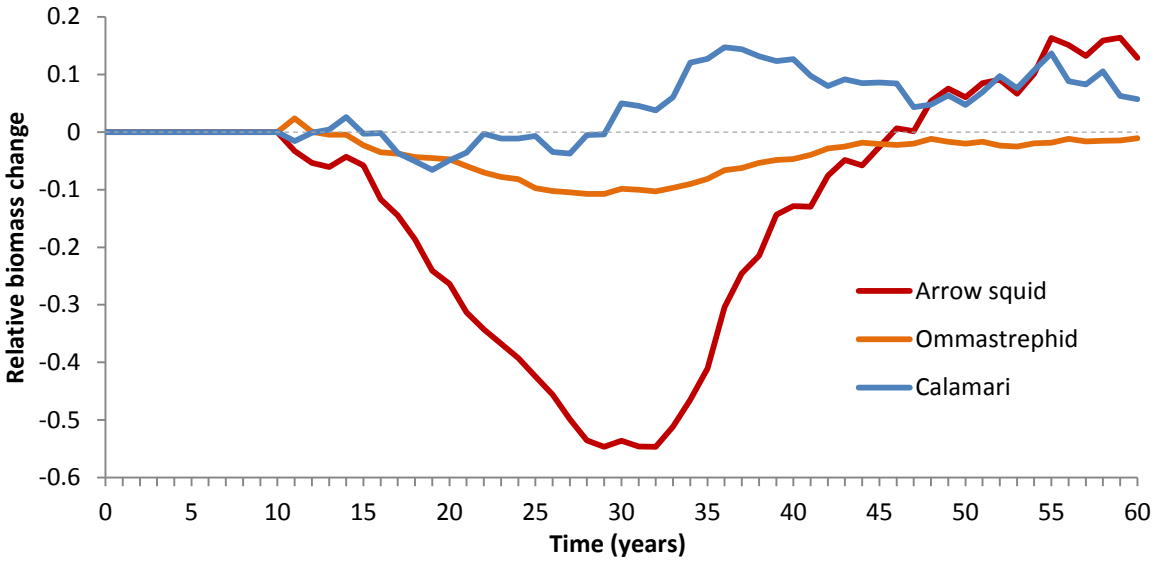


Figure 4-3: Relative biomass change of squid groups between the base scenario and the climate change scenario.

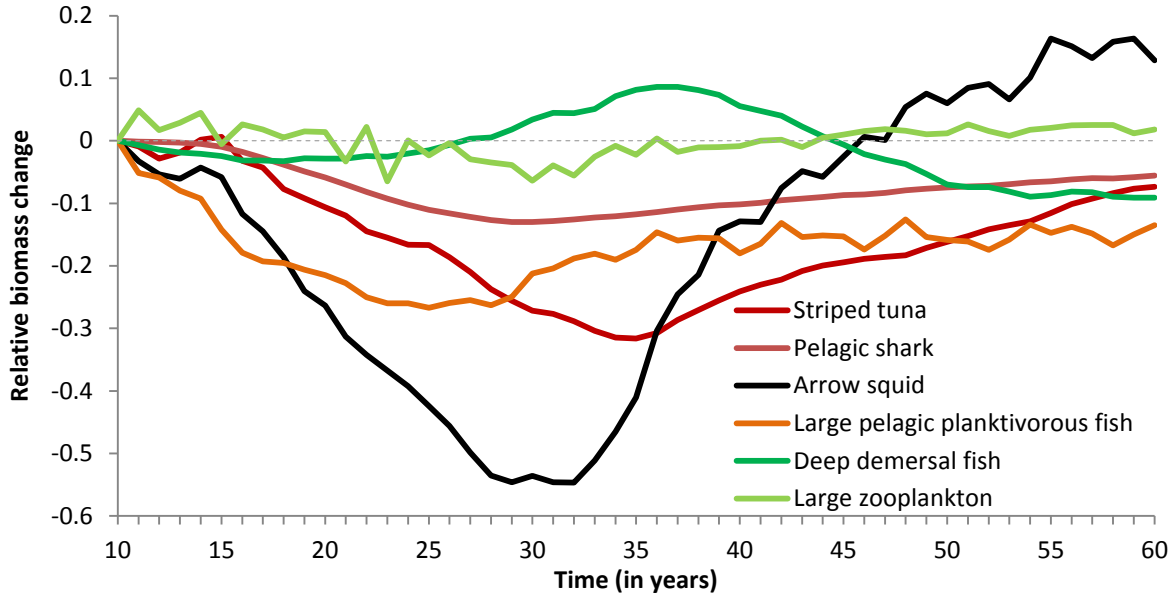


Figure 4-4: Biomass trends of arrow squid in its main predators and prey.

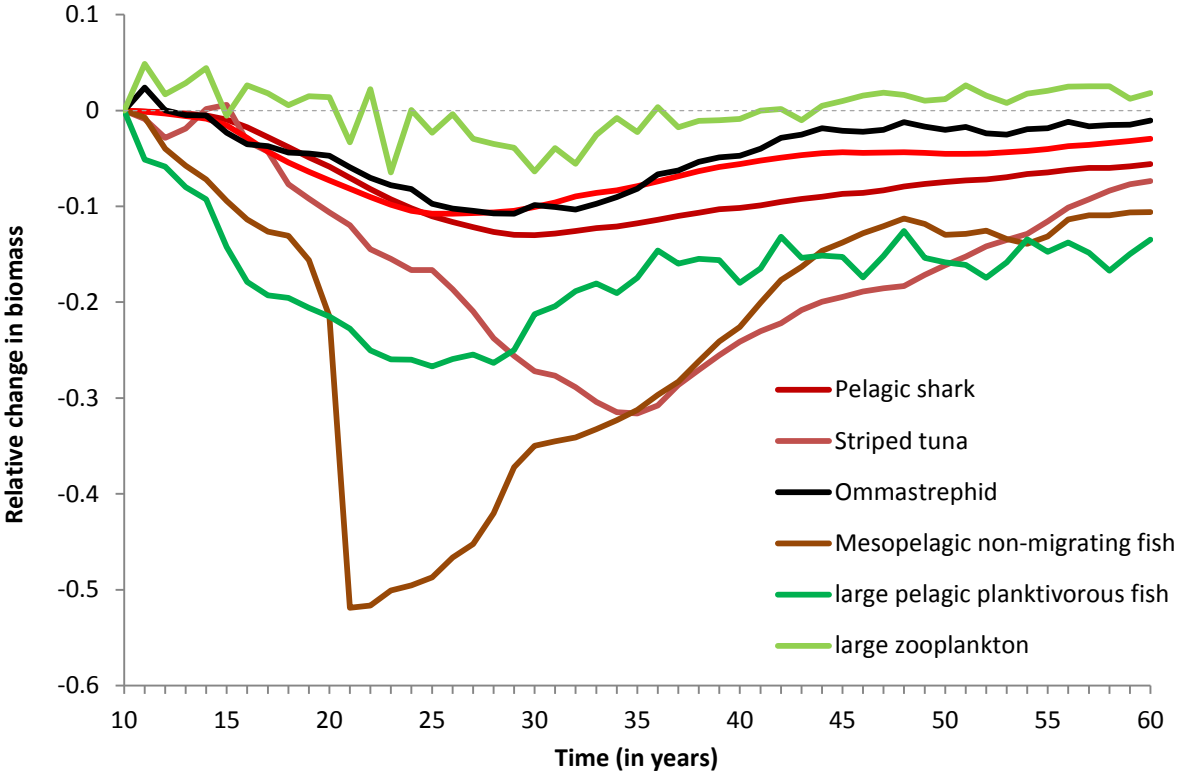


Figure 4-5: Biomass trends of the ommastrephid group and its main predators and prey.

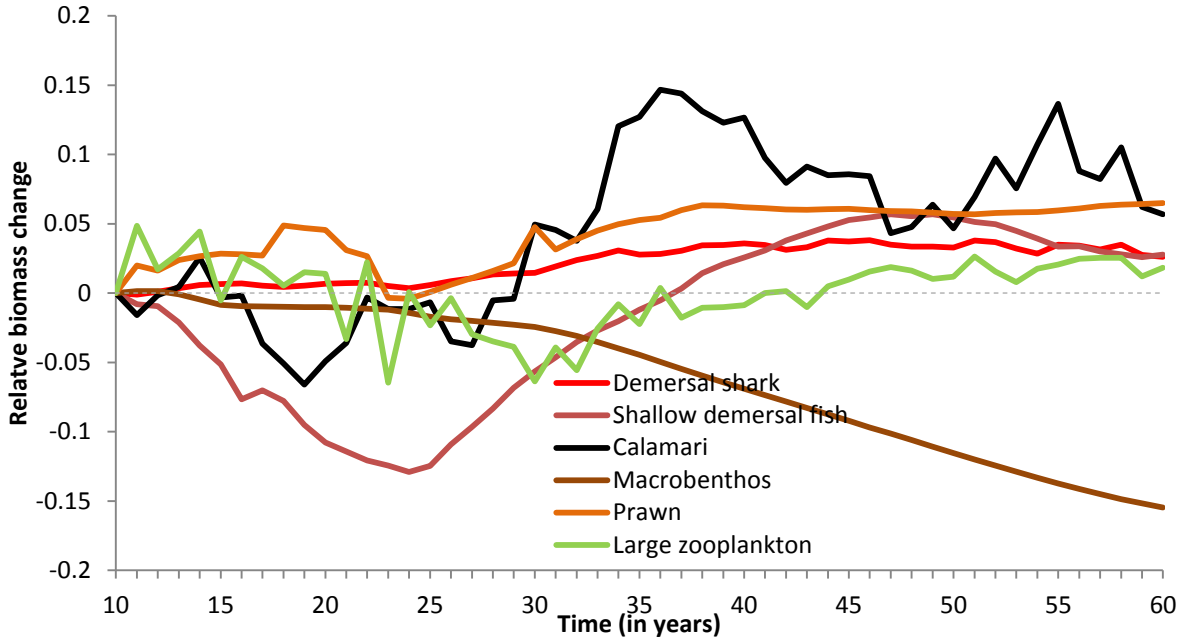


Figure 4-6: Biomass trends of calamari and its main predators and prey.

The diets of the various groups of the model show little change between the two scenarios (Appendix 4-6 and 4-7). The species that compose a large part of squid diets are the same (appendix 4-6a and 4-6b), and their importance in the diet do not change by more than 7% of the total diet (appendix 4-6a). For the arrow squid, the importance of prawns, squids and large zooplankton in adult diet is increased by the temperature change, while fish groups and benthic invertebrates represent a smaller part of the diet (appendix 4-6a). The ommastrephid group shows the smallest change in diet among squid groups (appendix 4-6). The strongest changes are in the diet of calamari (appendix 4-6), with megazoobenthos (stomatopods, starfishes, gastropods and other crustaceans) increasing by 7% of the total diet and prawns increasing by 3%. The parts of fish groups, zooplankton and other benthic crustaceans in calamari diet all decrease in smaller proportions (from 4 to less than 1% of the total diet). Predators of squid species, on the contrary, can show a more substantial change in their diets when the temperature is increased (appendix 4-7). The importance of arrow squid in the diet of mesopelagic predators (swordfish, albacore tuna) increases from 22% to 49%, while epipelagic fish prey are reduced from 45% to 22% and shallow piscivorous fish from 22% to 15%. In contrast, the diet of small whales, one of the main predators of the ommastrephid group, the diet changes very little. Demersal top predators showed various changes in their diet. For the main predator of calamari,

the demersal sharks, the importance of snapper decreases from 44% to 30%, while the neritic squid, crabs and shallow piscivorous fish all increase.

The physiological characteristics of the squid groups, or their condition, are slightly changed by the introduction of the climate change perturbation (Appendix 4-8). All groups have a diminution in size, although very limited. The calamari group is the one with the strongest reduction as their weight is decreased by 6.58%. Ommastrephid suffer a similar reduction and their weight goes down by 5.13%. The arrow squid diminution in size is the smallest as their weight is reduced by 3.26%. The ration between the reserve weight and the structural weight of the groups do not show any substantial change.

Discussion

The trends of secondary production in the system caused by the climate change scenario have a strong bottom-up impact on the food-web (Appendix 4-4). The squid species are both competitor and predator of several groups of forage fish in the model. Juveniles and young adult squid feed largely on zooplankton, which are a key food resource for forage fish, while adult squid prey substantially on planktivorous fishes (mackerel, sardines, anchovies) and mesopelagic fish (myctophids) (Appendix 4-6). This ontogenic change in squid diet occurs within a year and prevents forage fish groups from completely benefiting from the increase of any common food resource. The temperature increase in the climate change scenario explored with our model led to a change in the ecosystem functioning, with squid exerting a strong control on forage fish abundance and thus on the system,. The resulting increased predation that blocks on the recovery of forage fish abundance is reflected in the change in their biomass, and in their reduced importance in the diets of oceanic squids and other predators (appendix 4-6 and appendix 4-7), driving a decrease in biomass of many top predators (appendix 4-4).

Oceanic groups of intermediate trophic levels like large and small planktivorous fish (mackerels, sardines and anchovies), oceanic squids (ommastrephid and arrow squid) and mesopelagic forage fishes (myctophid and lightfish) all have their biomass decrease (figure 4-4 & 4-5, appendix 4-4) in the short term as they suffer from the decrease of food availability driven by an initial reduction in primary and secondary production. In the medium to longer term, however, these groups ultimately recover, though at different rates, as the secondary production rebuilds and eventually overtakes the level seen in the baseline model. However, the oceanic forage fish recovery is only partial, unlike the arrow squid that is both their predator and competitor and reaches abundance reaches substantially greater (by about 15% the baseline scenario) after 50 years of increasing temperature (fig 4-3 and appendix 4-4). This wide spread effect on many forage groups is also reflected in the top predators like sharks, tunas and carnivorous mammals. For the oceanic top predators there is some change in

predation on squids or on other fishes (appendix 4-7), but this is not sufficient to counter the effects of the decrease of availability of their main prey.

Ommastrephid squid, which also prey on and compete with oceanic forage fish, also show a dip before rebuilding, though not reaching the abundance seen in the baseline scenario (fig 4-5). Many oceanic top-predators like tunas suffer largely from the reduction of forage fish biomass (appendix 4-4). Predators actually feeding on squid species in the model (pinnipeds, small whales, striped tunas and mesopelagic predators like swordfish) have a much lower decrease in abundance, but still suffer a biomass reduction of 3% to 6%. The opportunism of squids, their fast growth and rapid turn-over compared to fish supports a high productivity potential and gives them the advantage and drives them to partly take the trophic niche left vacant by the decrease of forage fishes. However, even if some top predators switch at least some of their diet to squid species, there is still a change in the food web as the reduction of forage fish availability is generally detrimental to them (i.e. there is insufficient uptake of cephalopods in the predator diets to neutralise the loss of forage fish).

The results interactions between squids and forage fishes support the results from the qualitative model made by Bulman et al. (2011). This qualitative model also points at the negative impact of squid species on forage fishes and the associated effects on top predators. Local end-to-end models subjected to RCP8.5 scenario also showed a decrease of forage fish abundance and a biomass trend of squid similar to our results on arrow squid in terms of direction, although the magnitudes differ (Fulton & Gorton 2014). The abundance of squids in the model in Fulton & Gorton (2011) seems to explode after 40 years under the RCP8.5 scenario, and reaches about 10 times the biomass of the base scenario which is much higher than our predictions. This could be attributed to the very different implementation we developed in this model. Our approach of representing several cohorts per year probably makes squid groups sensitive to seasonal changes in a more realistic manner and therefore less sensitive than the gross aggregated biomass pool representation by Fulton & Groton (2011) in their consideration of the long-term temperature increase of the RCP scenarios tested. These comparisons of results are however limited as the analyses in publications seem to have a more

generalist approach and show results that group squid species like arrow squid and calamari together (Fulton & Gorton 2014).

In the neritic food-web, the biomass of neritic squid follows a different trend to that of oceanic squids. Under climate change, the abundance of neritic squid does not show a decreasing trend, instead growing above the levels seen in the baseline scenario, although only by about 10% (fig 4-6). These neritic squids do not suffer too much from the initial reduction in secondary production, probably because several of their other important prey, such as prawns and macrobenthos, do not undergo the same trend. Crustacean biomasses do not suffer substantial reduction in the first 30 years of the modelled time period and prawn biomass increases throughout (appendix 4-4 and fig 4-6). This increase in biomass of lower trophic level groups like prawns and zooplankton exerts a positive bottom-up effect on the neritic squid (and some of the other predators of the neritic food web like piscivorous demersal fishes or demersal sharks). The response of neritic groups is, however, more variable than in the oceanic food webs (appendix 4-5). The increase of several intermediate trophic level groups like neritic squids, warehous and trevalla puts downward pressure (via predation) on prey groups like crustaceans, but is beneficial for top predators, as the guild acts as a wasp waist connection in the system (Libralato et al. 2006; Shannon 2000). The diet changes of predators can be linked to the prey biomass changes. The increase in abundance of calamari and benthic feeders in the diets of demersal sharks supports their biomass increase, while their predation on crabs enhances the reduction in biomass of the crab group (appendix 4-7). This combination leads to some substantial biomass reductions in the reef associated fishes like wrasse species or banded morwong. It should be noted that some demersal groups are also sensitive to the arrow squid top-down control and thus show the opposite biomass trend as this squid species (fig 4-4).

The results of our model show the very different sensitivity and response from squid groups to the forcing of a temperature increase, even though they show a global increase in abundance (fig 4-3).

These differences can be explained by the relative productivity potential of each group. The greater voracity and frequent cohorts of arrow squid in our model makes it highly sensitive to bottom-up control from secondary producers, which results in a relatively high productivity. Neritic squid productivity is associated with their response to changes and to the various responses of their neritic prey. In total, these two groups benefit from the implemented perturbation, and the system shifts when the temperature increases by about +4% (from +0.4°C to 0.7°C depending on the area).

Despite adding a temperature scalar on the growth of the modelled species, to represent the effects of the shifting environment on the niche of species, the feeding processes and opportunism of squid species appear here to be the driving factor of squid response to our forcing. The modification in growth of squid species due to the temperature change is indeed relatively small, and is negative (appendix 4-8), even for the calamari, which had relatively strong temperature scalar compared to other groups of the model. Feeding activity is still the main driver of growth in the model, and the positive effect of a small temperature increase (fig 4-2) is hindered at first by the decrease of prey. At the end of our scenario, the growth of adult arrow squid and ommastrephid is limited by the reduction of forage fish biomass, and adult neritic squid growth suffers from the reduction of large crustacean groups. The increase of biomasses in our model is instead due to an increase in numbers more than in individual weights or conditions, as I show that individual size of squids is not substantially changed by our climate change scenarios (appendix 4-7 and appendix 4-8). Changes in abundance, more than in weight, size or condition of predator or prey, were thus the drivers of the small diet changes observed. This reflects the strong influence of trophic niches compared to abiotic niches in the populations dynamic and distribution on our model. This is a new insight into the interactions and trade-offs between these ecological constraints as the comparative influence of abiotic factors versus food availability are still highly uncertain for cephalopod species (Pecl et al. 2004; Pecl & Moltschaniwskyj 2006).

These conclusions regarding the representation of the trade-offs and interactions between trophic niches and environmental niches should be taken with caution however, as they are limited by the scarcity of information on abiotic niche studies. In many cases, I had to resort to the environmental conditions at the current distribution limits of some species, and use these values to constrain the niche. However, it is possible that the modelled group could live in a wider set of conditions than expressed today as they are potentially being (cryptically) limited by other biotic factors. Research on the physiological limitations of species would provide more robustness to our results.

Similarly, the limitation of our perturbation to a temperature change hinders our understanding of the full impact of climate shifts on ecosystem functioning. A temperature differential between the standard hydrodynamic forcing and the downscaled model caused confounding restructuring of the microbial foodweb in the most northly spatial divisions, which ultimately created numerical instabilities in the ecosystem model. Consequently, to maintain full control of the climate scenarios I elected to take the temperature anomaly approach – using the anomaly from the downscaled product and applying it to the standard hydrodynamic forcing to obtain the climate runs used in this study. This does omit any shifting transport (current flow) patterns in response to climates and focuses solely on temperature effects. The anomaly method (with no associated current shift) saw little spatial differentiation in the representation of the climate change driver pattern(s). This is likely why our results showed little variability in response across the area of focus, and may hide the true level of local variability in the responses of species (Stark 2008; Triantafillos 2002). However, given the primary focus of this piece of work was on the implications of the temperature effect, this approach was considered valid for this initial consideration of climate effects and cephalopod dynamics. Nonetheless, the representation of changes in oxygen levels and acidification processes in the model could bring valuable insights and precision to our predictions. The changes of oxygen levels in Gulf of California is for example believed to cause a shoaling of species distribution, bringing additional prey into jumbo squid foraging grounds and supporting its recent range extension (Stewart et al. 2013).

The strong uncertainty of the biomass estimates of cephalopod is also a substantial limitation on the robustness of our model results. Despite the large amount of research on cephalopod species, the relatively small scale of local cephalopod fisheries prevents the collection of exhaustive data across time and space. Applying our methods in regions where the model's parameters can be estimated and the model fit to longer time series would lead to less uncertainty around the results and could provide more insights regarding the mechanisms driving cephalopod and ecosystem functioning. A comparison between resulting models and our work would give us the opportunity to identify and maybe quantify the errors caused by biomasses uncertainty, but also to look for common patterns expressed across models and modelled systems.

If this study shows the benefit of the increase in temperature for squid species, occasional cooler years or events might have a more important impact on sensitive short-lived species like cephalopods than on other species. This highlights why studies need to move beyond considering average change to embracing climate variability, a topic that has received increasing attention over the last few years (Franzke et al. 2015). Introducing such events might lead to changes in our forecast.

A future research focus on the balance between neritic and oceanic food web, or between large groups of high biomass and single species groups of small biomass could also be extremely valuable. A number of demersal cephalopod species in Australia only have small biomass levels, but are nevertheless, important to system understanding due to their propensity for range-shift. Having the capacity to effectively represent octopus species such as *O. terticus* would allow for more indepth study the mechanisms driving or facilitating the range-shift of this species (Ramos et al. 2014; Ramos et al. 2015) and the potential effects on ecosystem functioning (Marzloff & Melbourne-thomas 2017).

While this study has focused on a single driver - climate – future work should tackle other drivers (e.g. fishing pressure) and how these interact – ultimately painting a picture of cephalopod resilience to cumulative stressors. Nevertheless, even as is our work may provide useful information for fisheries. Ecosystem management involves setting system level objectives and then using fisheries (and other) management controls to help guide ecosystem level outcomes in the desired direction. If the increase in abundance observed in the model and many other studies holds, it would suggest a potential opportunity for fisheries, though this should be considered with caution as the sustainability of cephalopod stocks under multiple stressors is as yet poorly understood and globally there were important drops in catches 2017 and 2018 (FAO 2018). These drops are believed to be caused by a combination of high fishing pressure on spawning biomass and weak recruitment due to poor environmental conditions. This may point again at the need to include exceptional events in our models. More generally, the comparison of various management strategies involving capture quotas, spatial or seasonal limitations or effort control could help increase the efficiency of fisheries exploitation while preserving the resources (Fulton et al. 2007).

Thanks to the focus on the representation of cephalopod ecology, this study brings new insights on the influence of cephalopods on ecosystem changes. This work also shows that with careful thought as to the representation of cephalopods in models, ecosystem models can successfully be used to assess potential future changes, despite the modelling challenges presented by cephalopod biology and ecology. A partial take-over of squid species as the connector of a wasp waist ecosystem can indeed be observed here. As the temperature starts rising substantially after 30 years, the biomass of producers of the system is increased. Squid species appear to react faster than many fish groups to the resulting bottom-up effect, due to their high voracity and frequent recruitment. By the end of the 50 years increase of temperature, arrow squid group biomass is increased by about 15%, calamari biomass by about 9% and the biomass of the ommastrephid group is almost back to its initial value despite the early decrease. The forage fish groups in particular suffer from this change as squid groups are both competitor and predator of these species. This results in a substantial reduction in abundance

of these groups and a widespread decrease in biomass of the oceanic food web. This work thus points at some of the mechanisms that could drive the dynamics of cephalopod ecology, and in a wider perspective influence the functioning of ecosystems as they are subjected to climate change. There is however still room for improvement for research on this topic. A broader consideration of oceanographic changes linked with climate change would bring robustness to the results of the model, and a more detailed representation of fisheries behaviours and dynamics would give valuable insights in a fisheries management and marine resource exploitation perspective.

Chapter 5 General discussion

Conclusions on cephalopod in models and role in ecosystems

Cephalopods are highly sensitive to many biotic and abiotic factors including environmental conditions (Green 2011) and food availability (Nishikawa et al. 2014). However, disentangling the effects of the different influences of the various factors in *in situ* studies has proven difficult, due in large part to the complex interactions between these factors and the resulting necessity for long term and extensive data sets (Stark 2008; Triantafillos 2002). Laboratory experiments, on the other hand, suffer from a lack of realism due to the limits of ecological dimensions considered or to a behavioural bias occurring (Moltschaniwskyj 2004). Mechanistic models, although they are far from solving all questions on ecology, allow us to incorporate information from laboratory and field studies and investigate the implications of hypothetically altering the system of a species of interest and other groups of the ecosystem, giving us an exceptional opportunity to confront these strategies and mechanisms in a global framework.

The limits of single species assessments are well recognized today (Hollowed et al. 2000; Quinn & Collie 2005), and complex ecosystem models provide us with a tool to simulate system-level experiments that would not be possible otherwise. These tools have been incrementally developed and refined as the basis for experimentation over (primarily) the past 3 decades, and in their current state offer us an opportunity to improve our system-level understanding and to investigate potential system' states and futures. They allow us to identify the roles of various species in the ecosystem and to specify the trophic structure of a food web. They can highlight unidentified indirect effects and processes and their consequences on the whole system. The work in this thesis is a valuable step towards the improvement of cephalopod representation in such models, an issue that was substantially limiting the capacity of these models, as cephalopod species are believed to have a strong impact on marine ecosystems in many regions of the world (chapter II). The insights provided by this work on

2159 the ecology of cephalopods and their role in the structure and function of ecosystems can be useful for
2160 anticipating the changes in our marine ecosystems over the future decades.
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2162
2163 In expanding the capacity of models to represent cephalopod life history and ecology my work was
2164 based on the most reliable information sources – the most widely documented species and processes.
2165 This approach has allowed for the addition of the representation of particular cephalopod traits –
2166 particularly for the squid groups covered by extensive bodies of available literature (i.e. *N. gouldi*, *S.*
2167 *australis*). The representation of four different life history stages allows us to model processes like the
2168 exponential growth and the multiple spawning events each year as the different cohorts reach
2169 maturity. The combination of these multiple stages with the opportunistic predation model
2170 formulation also results in a substantial ontogenic diet shifts that are specific to cephalopods. The fast
2171 growth and high voracity of our modelled groups also allow us to represent the dependence of the
2172 arrow squid abundance on the producers of the system and the resulting seasonal dynamics observed
2173 by local studies (Stark 2008). These results all confirm the potential of the newly modified ecosystem
2174 models to successfully represent cephalopod ecology.
2175
2176
2177 The research presented here demonstrates the influence of appropriately representing the ecological
2178 particularities of cephalopod taxa within an end-to-end model, and allows new conclusions and
2179 insights on the impact of cephalopods in the South East Australian system. While this more refined
2180 model confirmed the general picture compared to earlier models of the region, it allowed for a more
2181 in-depth analysis of the hypothesis that the impact of oceanic squids on the oceanic food web is
2182 substantial, but secondary to other groups as forage fishes are the main prey of oceanic predators and
2183 support the major part of the nutrient transfer through the oceanic food web (Bulman et al. 2011;
2184 Johnson et al. 2013). The impact of both squid groups of interest on the neritic food web is less
2185 important, and more dependent on the trophic links of each group. This work points at the growth
2186 capacity of squids as the key process regulating their impact on other groups of the system, as it

controls the trophic links of individuals, their activity and reproductive capacity. However, the forcing of an increase of temperature shows a substantial change in the ecosystem food web. The strong sensitivity and response of some squid groups to the bottom-up effects from producers of the system (Chapter III) gives them a competitive advantage, allowing them to benefit from the eventual increase of primary and secondary production in the system to a level beyond that of other groups. This results in a substantial decrease in the abundance of the forage fish and oceanic groups, as squids exert a top-down control and compete with the forage fish and other groups, taking over part of their trophic niche in what could be considered as ecological opportunism. Despite the modelled effect of temperature on the growth capacity of cephalopods, the impact of the temperature change on growth is very limited, and the trophic links of the groups rather than their environmental niche plays the key role in their response to perturbation. If the accurate representation of cephalopod growth is a key to modelling their impact on the system, their opportunism and voracity are the drivers of their ecological changes and have to be modelled adequately to consider marine food web dynamics. The various roles of squid groups in the model – and their different responses to perturbation – highlights the importance of representing the different cephalopod species based on their ecology, not only as a research and modelling exercise but for a better understanding of ecosystem functioning and for assessing their changing role under climate change.

Limitations

The high level of complexity of the Atlantis modelling framework allows us to represent intricate phenomena, but this type of model consequently has high computational demands and requires significant volumes of data. Moreover, such models generate complex results and their analysis requires time and caution. For this reason, it is very important to envisage the benefits brought by any increase in complexity before investing research means, and to assess the potential value of any results before investing the resources and deepening the work. Ultimately, results should be confronted with observations and be seen to yield valuable insights and information (the addition has

to be worth it to become a general addition rather than a novel and occasional inclusion for curiosity or some specific purpose), otherwise additional complexity can be considered an unnecessary cost.

Even though our model is based on a region where the availability of cephalopod data was relatively high (chapter II), I still had to use the calibration process to estimate some of their parameters, including their biomass. Additionally, the complete lack of abundance estimations makes it difficult to calibrate the biomass of cephalopod groups. Their biomass is thus estimated based on their abundance in predator's diet, which depends on several other parameters like predator abundance, habitat overlap and predator activity. This increases the uncertainty over our 'guesstimates' (estimates based on expert opinion and on the calibration process) of the biomass of cephalopod species, and requires a substantial amount of information on the ecology of their predators. In the case of the South East Australian region, the availability of studies on the ecology and diet of predators (appendixes of chapter 2) provides enough information to parameterize cephalopods in a realistic manner, but it should not be seen as a replacement for direct abundance estimates. The main cephalopod related process suffering from a lack of information is their reproductive dynamics. Atlantis generally bases this dynamic on a stock-recruitment relationship, something that is often weak for cephalopod populations (Bakun & Csirke 1998; Lipiński et al. 1998; Pierce & Guerra 1994). However, it was demonstrated here that it is still possible to realistically capture these early life history processes and build a model where this recruitment can be strongly dictated by other factors, such as food availability for juveniles (chap.2). Studies support the strong influence of this factor on recruitment success for Arrow squid in South East Australia or for *Ommastrephes bartramii* off the Japan coast (Nishikawa et al. 2014). While significant progress was made, this type of study is preliminary and more work is needed to refine our understanding of the recruitment mechanics of many cephalopod species around the world (Pierce & Guerra 1994). Moreover, the lack of robustness of any abundance estimates inevitably generates a strong uncertainty around the influence of the drivers of recruitment. Our representation of the dependence of *N. gouldi* abundance on food availability for juveniles could

be underestimating, or overestimating, the link between oceanographic conditions and squid population.

The growth of many cephalopod species is relatively well studied by looking at size-at-age based on the observation of statoliths (Jackson 1990; Yatsu 2000). However, the high intra-specific variability of their growth (Jackson et al. 1997; Hatfield 2000; Villanueva 1992) points at the necessity of considering the various factors influencing this growth. The identification of key drivers like food availability or pH is rare, and often only temperature is considered. Considering the important role of growth on cephalopod life-cycles, a good understanding of its drivers is very important to anticipate future changes in their ecology. Diet, assimilation and movement of the species of interest should be the next focus to complete and reinforce the robustness of ecosystem models. These traits have an impact on our view of the trophic interactions of cephalopod species and their capacity to transfer nutrients from lower to upper trophic levels of the food web. Finally, the effects of abiotic factors on the physiology and fitness performances have been proven difficult to tackle. They appear to have different effects at various life-stages, and are difficult to segregate from one another (Steer et al. 2007).

The collection of information about the sensitivity of some species to external factors like temperature, salinity, oxygen or acidity could substantially improve our assessment of the ecological changes of cephalopods with environmental perturbations and our view of the consequences for systems functioning. In this regard, the number of studies in South East Australia on the life cycles of *N. gouldi* and *S. Australis* was a very valuable asset to this study as it provided a view of the key factors involved. They allowed us to build these groups with accurate parameters, and to calibrate them in the most realistic way. The importance of this calibration process should not be underestimated (Fulton & Gorton 2014; Plagányi 2007). It is the step where the user can adjust all the parameters according to the level of uncertainty so the model results are realistic. The use of

sensitivity tests on parameters is very important in this regard. It allows us to identify the limits to which we are able to push some life-history traits while ensuring realistic results. However, the lack of suitable available information on some parameters, particularly key parameters, can hamper our efforts to compare the model results to real world data, reducing our capacity to obtain a complete and robust evaluation of cephalopods role in the system. All these limitations point at various features of the model that could be substantially improved by further investigation.

The difficulties faced in modelling the octopus group limits our assessment of the overall role of the complete complex of cephalopods in the system, instead constraining it just to the squid species. Squids are believed to be the cephalopod species of major importance in the food web due to their higher abundance and trophic links compared to octopus species and other cephalopods. However, understanding the dynamics of octopus species in the ecosystem could still bring new insights on potential future responses to climate change. The climate-driven change in distribution of species, with many shifting into new areas and leaving others, and their interactions with key species in ecosystems, such as urchins or lobsters, could influence the structure of ecosystems (or significant sub-components); and may in the future be used as indicators of change in coastal food webs (Marzloff & Melbourne-thomas 2017; Ramos et al. 2015). In this regard, the capacity to accurately incorporate interactions between groups whose abundance differs by orders of magnitude still requires substantial work. Another possibility is the use of different modelling tools to separately assess the functioning of ecosystems based on the habitats of species of focus or based on the processes and scales of interest, and to subsequently couple these different models (Fulton 2010).

Future of cephalopods in ecosystems and in research

Cephalopods have taken advantage of their high adaptive capacities in the past. They were the first species to colonize the water column as they developed, through several evolutionary steps, including gas chambers in their shell (Ward & Martin 1978) allowing them to take off from the seabed

(Chamberlain 1993). In many parts of the world, we can find fossils of Nautilus dating back until the pre-Holocene era and fossils of their ancestors, of the Ammonites genus, dating back to the Triassic (Teichert & Matsumoto 2010). These occurrences show the extent of the colonization of the ocean by these early cephalopods. The cephalopods considered in this study are endocochleates and are the result of the reduction and interiorization of the shell by descendants of ammonites. This feature appears to have given them an intermediate strategy between the slow-moving protected nautilus and the fast fishes. The development of their buoyancy organ provided them with an early opportunity to colonize the water column, but its limitation of movement and propulsion is likely the reason why fishes today dominate the ocean thanks to their superior motility (Chamberlain 1993), and may be why endocochleates developed high level escape mechanisms and behaviours like jet propulsion, ink ejection or camouflage (Adamo et al. 2006; Derby 2007; Wells & O'Dor 1991). The genetic variability that allows the physiological changes mentioned above is not represented in models as yet and the anticipation of new traits seems difficult. However, the complexity and representation of numerous processes in an ecosystem modelling tool such as Atlantis would potentially allow us to represent many ecological changes resulting from such evolutions, and would give us an incredibly valuable insight on the effects of these new traits on species interactions and ecological evolutions.

Coastal and temperate areas like South East Australia show the highest uncertainty and variability in terms of biomass changes when models are subjected to climate change scenarios (Lotze et al. 2018). In these particular regions, changes are generally complex as they provoke changes in the specific composition of marine communities. The development of local ecosystem models with specific groups and relatively advanced representation of species' responses to environmental changes is thus necessary to understand ecosystem change over time in these zones. In these particular zones, the influence of cephalopod dynamics on ecosystem dynamics could be even more important to assess. Today, the observed general increase of cephalopod abundance around the world (Doubleday et al. 2016) could be combined with a forecasted decrease of abundance of larger animals of middle to upper trophic levels (Bryndum-Buchholz et al. 2018; Lotze et al. 2018). The development of squid

representation in other ecosystem models would allow us to identify systems where squid species influence and drive these changes via similar mechanisms. They would also potentially highlight the key features of systems in which these processes occur, allowing for generalization on more global scales.

Future research should focus on modelling cephalopod species with very different ecologies. As mentioned above, the inclusion of octopus species in the Atlantis framework still requires substantial improvement. Cephalopod species that do not appear to benefit from current changes in the model should also be considered. Some species are indeed classified as endangered on the IUCN red list. These species are believed to suffer from relatively slow turn-over and small recruitments compared to other cephalopod species. Clearly identifying the traits responsible for the different responses to external change could be a substantial step towards the identification of the necessary conditions and life-traits for the increase of cephalopod abundance. Similarly, applying our method of work to the population of *Illex argentinus* off the Falkland Islands or *Dosidicus gigas* along the West coast of America could bring valuable insights. The first species is a key component of a food web with relatively low predation from pelagic fishes, but a strong role of prey for top predators like penguins and mammals (Laptikhovsky et al. 2010), while the second is a squid species of particularly high trophic level acting as a top predator (Markaida & Sosa-Nishizaki 2003; Ulloa et al. 2006) that has been expanding its range in recent years (Field et al. 2007; Tennesen 2015). The insights from these two very different species and ecosystems could give new perspectives on the influence of specific life-history traits on the role of cephalopods.

The next step forward in the modelling of cephalopods in the South East Australian region is the inclusion of the oceanographic changes expected with climate change and the southward shift of the East Australian Current. These changes should strongly affect the producers of the system, and thus the dynamics of the food web, and more particularly the population dynamics of squid species that are

strongly dependent on the abundance of food availability for juveniles (chapter III). Similarly, there is a need to include extreme events in our scenarios and forecasts. Occasional years or seasons with extreme environmental conditions in the future will likely result in a temperature trend or nutrient inputs more variable than the ones used here to simulate the effects of temperature increase and climate change. These extreme events could have substantial impacts on short lived species like producers (Hallegraeff 2010), forage fishes or cephalopods, and therefore affect the results of our model.

Ultimately, the impact of fisheries should be the subject of more research and studies. Rising interest from fisheries stakeholders has driven the Australian Fisheries Research and Development Corporation (FRDC) investigate the possibility of developing local squid fisheries (Dunning et al. 2000). Squid and cephalopods are thus the topic of a significant number of FRDC publications, with the FRDC website listing squid related publications, as much as sardine (27). Nevertheless, this attention is still much lower than that received by finfish - as a comparison, there were 73 publications on mackerel, another forage fish, and 307 on tuna. Squid studies still amount to a relatively important research volume considering sardine in the year 2015-16 represented 44.000t and 29.7 million AUS$ and squids in the same period represented “only” 2.000t and 12.8 million AUS$.

The importance of squid to global fisheries cannot be denied, however, and the modifications and dynamics of fisheries and their impact on the cephalopod populations should be taken in account in future scenarios. These scenarios should test the effects of various management strategies aimed at regulating exploitation, such as considering spatial or periodic control of the activity, or focused on the effort intensity or on levels of total capture. All these levers, and their combinations, could have very different impact on cephalopod dynamics and on their role in the food web. Some early investigations have already been done testing the effect of increased removal of volume of squids (e.g. Johnson et al. 2013). However, these models typically only represented the effect of fisheries through

biomass removal (Johnson et al. 2013), and their representation of cephalopod ecology more broadly is relatively limited (Fulton & Gorton 2014). In a fisheries management perspective, scenarios and simulations should also be extended to the socio-economic dimension. In the South East Australian region, the profitability of squid fishing activity is related to several factors, from the concentration in time of local catches affecting market prices, to more global factors influencing the cost of the activity (McKinna 2011). All these factors affect fishing dynamics and impact the socio-economic sectors. Integrating these processes in to models would improve the representation of fisheries dynamics and the vision of decision makers when fisheries policies are discussed. At a global scale, a focus should be put on *I. argentinus* off South East American coast, *Todarodes pacificus* off the East Asian coasts and *D. gigas* off the East American coasts. These stocks represent the major part of cephalopod catch volume in the world (respectively 16.1%, 15.9% and 12.8% in 2002), captures are exported worldwide and the volume of catch of these species largely influences the price of cephalopod on global markets (FAO 2018; McKinna 2011).

Conclusion

The results of this work show that ecosystem models can be improved to reproduce some of the particular features of cephalopod ecology adequately. The model described in this volume successfully reproduces the voracity, the opportunism, the growth and ontogenic diet shifts of cephalopods that ecosystem models generally disregard. In the South East Australian system, these life-traits are driving the impact of squid species on the ecosystem. The mechanisms reveal oceanic squid dependence on planktonic prey for juveniles, and the key driving role of growth in squid ecology. The forcing of a climate change scenario involving a temperature increase in the region also reveals the capacity of squid species to outcompete many fish groups when producer abundance increases and to exert a top-down control on them through adult squid predation. This work is a valuable step towards an adequate representation of cephalopod species in ecosystem models, and towards the assessment of their impact on the system at a time when their abundance worldwide appears to be increasing.

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Appendixes

Appendix 2-1. Type of data and information on the ecology of cephalopods.

Data type/information	Insight on cephalopods role in ecosystems	
	Ecological processes touched	Comments
Abundance	Biomass	Suffer some bias as they are able to escape sampling gear. Robust estimations are scarce.
Distribution	Potential interactions and habitats	Suffer some bias as they are able to escape sampling gear.
Movements	Potential interactions and habitats	Studies are common in some regions and scarce in others.
Diet	Trophic interactions	Stomach studies [common] should be combined with isotope analysis [scarce] as beak ingestion makes stomach contents biased.
Consumption rate	Trophic interactions intensity and impact on lower trophic levels	Not common.
Consumption by predators	Trophic interactions intensity and importance for upper trophic levels Mortality Distribution	Predators stomach studies have to be combined with isotope analysis as cephalopod beaks have a longer retention rate than other remains.
Growth	Production	Common, but often restricted to sub-adult and adult stages.
Reproductive output	Production	Few.
Lifespan	Mortality	Common.

Information and insights gathered on the role of cephalopods. It should be noted that this knowledge is generally very species dependant, species of interest for fisheries or iconic ones are generally more documented than others.

Appendix 2-2. Ecosystem models and evaluation of cephalopods implementation and role in the system.

Implementation score: explanations are given in table 1. Please, note again that classifications are not reflecting the global quality or robustness of the models, they only represent an assessment of the adequacy of the model to assess the role of cephalopods, which may not be the point of interest in every study. For each area, the last model in frame is the one used in the map (the most adequate model with a role score available). We displayed here only the role score of the cephalopod groups with the highest score. A table with scores of the various cephalopod groups is displayed in the next appendix.

Area of focus and reference	Realisation year	Modelling framework	Implementation score		Role score	References
			data/ structure	global		
Benguela						
southern Benguela	1998	EwE	2/1	2		(Jarre-Teichmann et al. 1998)
southern Benguela	2003	EwE	1/1	1		(Shannon et al. 2003)
southern Benguela	2013	Atlantis	1/2	2		(Smith 2013)
southern Benguela	1999	EwE	2/1	2	3	(Shannon & Jarre-Teichmann 1999)
northern Benguela	1999	EwE	2/1	2	3	(Shannon & Jarre-Teichmann 1999)
Mediterranean Sea						
Catalan sea	2006	EwE	1/2	2		(Coll et al. 2006)
Catalan sea	2008	EwE	1/2	2		(Coll et al. 2008)
Ionian Sea	2010	EwE	1/1	1		(Chiara et al. 2010)
Adriatic Sea	2009	EwE	2/2	3	4	(Barausse et al. 2009)
Bay of Biscay						
Cantabrian Sea	2004	EwE	2/2	3		(Sánchez & Olaso 2004)
Bay of Biscay	2011	EwE	2/2	3	2	(Lassalle et al. 2014)
North West Atlantic						
Middle Atlantic Bight	2001	EwE	2/2	3		(Okey 2001)
North East US	2010	EwE	3/2	3	2	(Link et al. 2010)
South West Atlantic						
South Brazilian Bight	2004	EwE	2/2	3		(Gasalla & Rossi-Wongtschowski 2004)
Southern Brazil	2005	EwE	2/2	3		(Velasco & Castello 2005)
South Brazilian Bight	2010	EwE	3/2	3	4	(Gasalla et al. 2010)
South East Australia						

South East Australia	2007	Atlantis	3/2	3		(Fulton et al. 2007)
Eastern Bass Strait	2006	Atlantis	3/2	3		(Bulman et al. 2006)
Pelagic eastern Great Australian Bight	2011	Atlantis	3/2	3		(Bulman et al. 2011)
Pelagic Eastern Bass Strait	2011	Atlantis	3/2	3		(Bulman et al. 2011)
eastern Great Australian Bight	2011	EwE	3/2	3		(Goldsworthy et al. 2011)
South East Tasmania	2011	Atlantis	3/2	3		(Johnson 2011)
South East Australia	2012	Atl/EwE	3/3	4		(Fulton et al. 2012)
eastern Great Australian Bight	2013	EwE	3/2	3		(Goldsworthy et al. 2013)
South East Australia	2014	Atlantis	3/3	4		(Fulton & Gorton 2014)
Tasmanian waters	2013	EwE	2/3	3	4	(Watson et al. 2013)
California current						
gulf of California	2002	EwE	2/1	2	2	(Arreguín-Sánchez et al. 2002)
gulf of California	2004	EwE	2/1	2	2	(Morales-Zárate et al. 2004)
North California Current (NCC)	2006	EwE	1/1	1	4	(Field et al. 2006)
California Current	2007	Atlantis	3/2	3		(Brand et al. 2007)
gulf of California	2008	EwE	3/2	3		(Rosas-Luis et al. 2008)
California Current	2010	Atlantis	2/3	3		(Horne et al. 2010)
California Current	2012	Atlantis	3/2	3		(Kaplan et al. 2012)
NCC	2007	EwE	2/2	3	4	(Field et al. 2007)
Eastern Tropical Pacific (ETP)						
Eastern Tropical Pacific	2003	EwE	3/2	3	4	(Olson & Watters 2003)
ETP	2007	EwE	2/2	3	4	(Field et al. 2007)
Humboldt current						
North Humboldt Current	2008	EwE	3/2	3	3	(Tam et al. 2008)
North Humboldt Current	2008	EwE	3/2	3	3	(Taylor et al. 2008)
Humboldt central Chile	2013	EwE	3/2	3		(Neira & Arancibia 2013)
Humboldt central Chile	2005	EwE	3/2	3	3	(Arancibia & Neira 2008)
Antarctic						
Antarctic Peninsula	2008	EwE	2/1	2	1	(Cornejo-Donoso & Antezana 2008)

Bay of Bengal						
Bangladesh waters	2003	EwE	2/1	2	1	(Mustafa 2003)
South East India	2010	EwE	2/1	2	2	(Antony et al. 2010)
Bay of Bengal	2013	EwE	2/1	2		(Guénette 2013)
Bay of Bengal shelf	2012	EwE	2/1	2	1	(Ullah et al. 2012)
Atlantic Arctic						
Arctic Labrador & Newfoundland	2000	EwE	3/1	2		(Bundy et al. 2000)
South West Greenland	2001	EwE	1/2	2	1	(Pedersen & Zeller 2001)
Western North Pacific						
Western North Pacific	2014	EwE	2/2	3		(Mori et al. 2014)
Japan East Sea	2004	EwE	3/1	2	4	(Zhang et al. 2004)
Japan East Sea	2007	EwE	3/1	2	4	(Zhang et al. 2007)

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Appendix 2-3. Trophic studies on cephalopods role. Insight given on the trophic role of cephalopods in food webs by non modeling studies. We displayed studies of secondary consumers of our areas of interests and studies focused on cephalopods. The role of cephalopods as prey is shown by their importance in the diet of predators of the system. The width of their impact as predator can be analysed through their diet, but the intensity of this impact requires studies on their consumption and abundance that could be found in few areas.

Diet content is estimated with Index of Relative Importance (IRI) [150] if possible; percentage of stomach content weight; and numerical percentage when it is the only quantification available. Cephalopods are classified in predators diet as: major prey [top 3 IRI or part superior to 30%] secondary prey: [between fourth and tenth IRI or part between 10% and 30%; minor prey part inferior to 10%] or minor prey when their contribution is lesser. If fishes, crustaceans and cephalopods are around similar relatively high values in diet [between 25% and 35%] we mentioned a "balanced diet" instead of "major" groups and "secondary" groups in order to give a better representation of studies results.

GC: Gut Content; IA: Isotope analysis

reference	Study type and eventual focus	Predator looked at	Cephalopod importance for predators (from % of diet weight if possible or % of prey number) or diet of cephalopods
South West Atlantic			
(Arkhipkin et al. 2012)	GC	12 species of nektonic predators	Across all species: 2 sharks, 1 ray, 9 other fishes (mainly cods and perch-like). Squids (mainly loliginid *D. gahi*) represent 15% of total predators diet.
(Brickle et al. 2009)	GC	Hoki Blue whitting	*M. ingens* secondary prey (10% of diet volume) of adult hoki. No cephalopods in Blue whitting diet.
(Croxall & Wood 2002)	GC	6 seabird species and 2 seal species	Squids secondary prey (20 to 30%) of seabirds and marine mammals.
(Jackson et al. 2000)	GC	Southern opah	Specialised cephalopod feeder. Juveniles *M. ingens* (ommastrephid) present in 47% of individuals. *L. gahi* (Loliginid) represent 23% of prey. Other squids represent less than 1% of prey.
(Lopes et al. 2012)	GC	Guiana dolphin	Loliginids (mainly *L. plei*) is major prey of 1 Dolphin species (37%).
(Santos & Haimovici 1998)	*L. sanpaulensis* in GC	47 potential predator species	Present in 45 predators diet Major prey of 2 fish species, 5 marine mammals and 1 penguin species; Secondary prey of 1 fish species; minor prey of 16 fish species and 2 squid species and absent of 4 diets. Its major prey are Osteichthyes, Crustaceas are secondary prey and squids are a minor prey item.
(Santos & Haimovici 2000)	*I. Argentinus* in GC	67 potential predator species	Present in 32 predators diet Major prey of 5 marine mammal species, 2 billfishe species, 1 groundshark species; Secondary prey of 2 billfish species, 2 ground shark and 1 perciform speciess, Minor prey of 7 fish species, 2 squid species and 1 penguin species.
(Santos & Haimovici 2002)	Cephalopods in GC	71 potential predators	Loliginids are the main cephalopod prey of neritic marine mammals, penguins and dolphins. Ommastrephids are the main cephalopod prey of the slope area and adjacent oceanic water predators (wreckfishes, tunas, swordfishes, sailfishes, marlins)
Cephalopods			

(Arkhipkin et al. 2012)	GC	*D. gahi* *I. argentinus* *O. ingens*	Across all species: 2 sharks, 1 ray, 9 other fishes (mainly cods and perch-like), 3 squids Squids are key consumer of the system. *D. gahi* is responsible for about 50% of total consumption and *I. argentinus* is responsible for about 15%.
(Arkhipkin 2013)	Production and population model	*D. gahi* *I. argentinus* *O. ingens*	Key nutrient vector between trophic levels and between inshore and offshore area. The *I. Argentinus* has the strongest impact on ecosystem resources. *D. gahi* and *O. ingens* had a smaller but substantial impact.
(Brickle et al. 2001)	GC	*D. gahi*	L. gahi itself is an important prey item, but it is believed to be due to trawl feeding and not to natural behaviour. Crustaceans (krill, amphipods and chaetognaths) are major prey.
(Ivanovic & Brunetti 1992)	GC	*I. argentinus*	Crustaceans (mainly amphipods completed with euphasids) are major component of the diet (57%), while myctophids (29%) and squids (13%) (oceanic and neritic) are secondary items. Other fishes are minor items.
(Laptikhovsky 2002)	GC	*I. argentinus*	Crustaceans made 95% of the diet, squid 3%, fish 1%
(Santos & Haimovici 1997)	GC of squid	*I. argentinus*	Osteichthyes are major prey (43%) Cephalopods (28%) and Crustaceans (19%) are secondary prey
South East Australia			
(Coleman & Mobley 1984)	GC	52 fish species	Present in 21 predators Cephalopods are major prey item of 4 shark species, 1 flathead and 1 carangid; Secondary prey of 1 shark species, 3 bathypelagic fish species (macrourid, dory, flathead); minor prey of 2 shark species, 3 tuna species, 2 Searobin species, 1 Snapper, Snake mackerel, flathead and morwong species
(Davenport & Bax 2002)	IA	87 nektonic predators	*N. Gouldi* is a tertiary consumer. Prey of top consumers and predators of zooplanktivorous fishes.
(Evans & Hindell 2004)	GC	Sperm whale	Oceanic squids represent most of the diet. Onychoteuthid squids are the most prominent family (36%) followed by Architeuthids (17%) and Ommastrephids (7%). Other oceanic squids and octopods complete the diet
(Lansdell & Young 2007)	Cephalopod in GC	2 billfish species and Yellowfin tuna	Ommastrephids are by far the main cephalopod prey (60 to 80%). *O. bartramii* and *N. Gouldi* are the main cephalopod species prey of Swordfish Yellowfin Tuna cephalopod diet is composed mainly of various ommastrephid species Dolphinfish cephalopod diet is mainly based on *T. eblanae*
(McIntosh et al. 2006)	GC	Sea lions	Octopus (40%) and cuttlefish (30%) are major prey of sea lions; Ommastrephids (14%) are secondary prey; fish species are minor prey
(Pethybridge et al. 2011)	GC	15 Demersal sharks and chimaeras	Cephalopods (bathypelagic squids mainly, completed with ommastrephids) are major prey of 1 species and secondary prey of 3 others. Remaining species presented too few prey items to draw conclusions
	fatty acid		Squid species are the most prominent prey group. Myctophids and other fish are the next prey groups.
(Rogers et al. 2012)	GC	5 pelagic sharks species inshore	Cephalopods (mainly neritic squids and cuttlefishes) are a major item of 2 species diet and a secondary item of 2 others

			Oceanic squids (Ommastrephids) are secondary prey of the shortfin mako.
(Young et al. 1997)	GC	Bluefin Tuna	Inshore: Cephalopod (mainly *N. gouldi*) 14% Offshore: Cephalopod (various oceanic squid) 54%
(Young et al. 2001)	GC	Yellowfin Tuna	Oceanic squids (mainly *N. gouldi*) are a secondary prey (14%) Other squids are minor prey
(Young et al. 2010)	GC	10 large carnivorous fishes	Ommastrephids are major prey of 3 species, secondary prey of 3 others and minor prey of 4 others. Histioteuthids are a major prey of 1 species (Blue shark, also largely feeding on ommastrephids) and minor prey in all others. Other cephalopod species are minor prey or absent of the diets
Cephalopods			
(Braley et al. 2010)	GC	*N. gouldi*	Fish are major prey item (48%), crustaceans (mainly euphasid) (25%) and cephalopods (mainly ommastrephids) (22%) are secondary item
	DNA analysis	*N. gouldi*	Fish (mainly small planktivorous and piscivorous) (50%) and *N. gouldi* (38%) are major prey item; and crustaceans (mainly euphasids) (13) are secondary prey item
(O'Sullivan & Cullen 1983)	GC	*N. gouldi*	Balanced diet between fish (mainly pilchard and gemfish) (37%), crustaceans (mainly Caridae, Amphipods and Isopods) (36%), squids (ommastrephids) (26%)
(Pethybridge et al. 2012)	GC	*N. gouldi*	Teleosts (especially lanternfish and hatchetfish) (67%) and cephalopods (35%) are the main prey item. Crustaceans (8%) are a minor prey item
	Lipid and fatty acid	*N. gouldi*	Myctophid (mesopelagic fish), crustaceans and cephalopods are major prey
(Pethybridge et al. 2013)	GC	*T. filippovae*	Myctophid fish is the major prey group (63%); squids (mainly Onychoteuthids and Histioteuthids) (19%) are secondary prey items; crustaceans (14%) are secondary prey items
	Lipid and fatty acid	*T. filippovae*	Myctophid fish is the major prey group. Squids (mainly Onychoteuthids and Histioteuthids) are secondary prey items.
(Uozomi et al. 1995)	GC	*N. gouldi*	Fishes (mainly pilchard and sprat) (25% to 40%), squids (20% to 55%) and crustaceans (10% to 40%) are balanced in the diet
Western North pacific			
(Kubodera et al. 2007)	GC	Blue shark & Salmon shark	Cephalopods (51%) (various squid species) are a major prey item.
(Mori et al. 2001)	Squid in GC	Fur seal	Main squids are *Watasenia scintillans*, *Onychoteuthis borealijapanica* and *Ommastrephes batramii*.
(Ohizumi et al. 2003)	GC	Beaked whale	Squids (4%) (mainly oceanic squids) are a minor prey
(Watanabe et al. 2003)	GC	Pacific pomfret	Oceanic squids (50%) are a major prey item, small fishes are a secondary prey item, crustaceans, other cephalopods and other fishes are minor prey item.
(Watanabe et al. 2004)	GC of	Albacore tuna	subarctic gonatid squid, *G. borealis* (11%) is a secondary prey item

Cephalopods			
(Uchikawa & Kidokoro 2014)	GC	*T. pacificus*	Crustaceans (55%) (mainly amphipods) and fish (40%) (mainly Maurolicus japonicas) are major prey items, cephalopods are a minor prey item.
(Watanabe et al. 2004)	GC	*O. bartramii*	High seasonal variability. Cephalopods (mainly oceanic squids) (12% to 65%); crustaceans (0.1% to 85%) fishes (68%).
Bay of Biscay			
(Chancollon et al. 2006)	GC	Swordfish	Confirm importance of oceanic squids
(Clarke & Stevens 1974)	Cephalopods in GC	Blue shark	Cranchids, Ommastrephids and Cuttlefishes all represent more than 20% of cephalopods. Octopods and other squids are a minor part of cephalopod prey.
(Das et al. 2000)	IA	Albacore Tunas 2 Dolphin species	Cephalopods are important prey of Tunas Cephalopods are secondary or minor prey of Dolphins
(Guichet 1995)	GC	Hake	Minor prey
(Logan et al. 2011)	IA and GC	juveniles Bluefin Tunas	Minor prey
(Pusineri et al. 2008)	GC	3 billfish species, blue shark, albacore tuna	Oceanic squids species are major prey
(Spitz et al. 2011)	GC	9 ondocetes species	Important prey of ondocetes predators
(Velasco et al. 2001)	GC	27 demersal fish species	Minor prey of demersal fish community
Cephalopods			
(Guerra & Rocha 1994)	GC	*L. vulgaris*	Fish 75% (mainly sand lances), Crustaceans 10%, Polychaetes 9%, Molluscs (mainly loliginids) 7%
		L. forbesi	Fish 68% (mainly sand lances), Crustaceans 21%, Molluscs (mainly loliginids) 11%
(Rasero et al. 1996)	GC	*T. eblanae*	Fish (mainly Blue Whiting) 90%, Cephalopods 7%, Crustacea 3.5%
		I. coindetii	Fish (mainly Blue Whiting) 77%, Crustacea 12%, Cephalopods 11%
(Lordan et al. 2001)	GC	*T. sagittatus*	Fish (small planktivorous fishes) 84%, Crustacea 14%, Cephalopods (oceanic squids) 2%
Bay of Bengal			
(Maldeniya 1996)	GC	Yellowfin tuna	Cephalopods are major prey of adults and secondary prey of smaller individuals
(Nootmorn et al.	GC	5 pelagic apex	Squids are major prey (61%)

2008)		predators	
(Rao 1964)	GC	39 fish species	Cephalopods are major prey of 4 species and minor prey of 4 others
(Rao 1981)	GC	Lizard fishes	Cephalopods are absent
Benguela			
(Rohit et al. 2010)	GC	Yellowfin tuna	Squids (*S. oualaniensis*) are secondary prey (16%)
(Lipinski 1992)	GC	17 groundfish species	Squids and cuttlefishes are secondary prey of hakes
(Meyer & Smale 1991)	GC	12 demersal teleost predators	Cephalopods are minor prey of 8 species and absent of 4 species
(Smale 1986)	GC	6 pelagic teleosts predators	*L. reynaudii* is major prey of 1 species, secondary prey of another and minor prey of 2 other species Ommastrephids are secondary prey of one different species, minor prey of another and minor prey of a species also feeding on *L. reynaudii*
Cephalopod			
(Lipinski 1992)	GC	4 squid, 1 cuttlefish and 1 octopod species	Predators of lightfishes, lanternfishes, hake, shrimps, stomatopods. Prey of numerous fish species, seals, sharks and cetaceans
(Sauer & Lipiński 1991)	GC	*L. reynaudii*	Teleosts (mainly codlets and hake) (58%) are major prey; crustaceans (25%) are secondary prey and cephalopods (3%) are a minor prey
Mediterranean Sea			
(Pedà et al. 2015)	GC	35 marine mammals	Pelagic squids: major prey of 3 species of marine mamals Demersal octopuses: major prey of bottlenose dolphin only (*Tursiops truncatus*)
(Peristeraki et al. 2005)	Cephalopods in GC	Swordfish	Oceanic squids: Important prey of Swordfish Neritic squids: Secondary prey of Swordfish
(Quetglas et al. 2010)	GC	2 Histioteuthid species	Histoteuthids: Predators of small fishes, mainly myctophids, and crustaceans
(Salman 2004)	GC	Swordfish	Cephalopods are secondary prey (17%). Balanced part of squids, cuttlefishes and octopods
(Stergiou & Karpouzi 2002)	GC	146 fish species	146 species: important prey of upper trophic levels of the system.
Cephalopods			
(Quetglas et al. 1999)	GC	*T. sagittatus*	Important predators of Osteichthyes (60%), cephalopods (18%) and crustaceans (21%) are secondary prey
North West Atlantic			
(Logan et al. 2011)	GC & IA	juveniles Bluefin	Minor prey

		Tunas	
(Chase 2002)	GC	Bluefin tuna	Squids and octopods are minor prey of adults Bluefin Tunas (2%)
(Gannon et al. 1997)	GC	Lon finned pilot whale	Loligo pealei 73%, Ommastrephids 12%, Histioteuthids 7% Other squids and fish are minor prey items
(Stillwell & Kohler 1982)	GC Shortfin mako	Shortfin mako	Cephalopods (mainly omamstrephids) are minor prey item: 1.3%
(Staudinger et al. 2013)	GC	12 fishes [teleosts & elasmobranchs]	Oceanic squids are major prey of 6 species; secondary prey of 5 species; minor prey of 1 species
Cephalopods			
(Hunsicker & Essington 2008)	Consumption model	*L. pealei*	Neritic squid could have a stong trophodynamic impact on carnivorous fish recruitment (Haddock, cod, hake, flounder and Butterfish)
(Maurer & Bowman 1985)	GC	*L. pealei* & *I. illecebrosus*	*Illex illecebrosus* and *Loligo pealei*: seasonal changes in diet with crustaceans (mainly euphasids), fishes and squids
California gulf			
(Abitía-Cardenas et al. 1999)	GC	Blue marlin	Jumbo squids is a secondary prey (10.3%)
(Abitía-Cardenas et al. 2002)	GC	Striped marlin	Jumbo squids is a minor prey (7.7%)
(Ruiz-Cooley et al. 2004)	IA	Sperm whale	Jumbo squids are prey of sperm whale
Cephalopods			
(Ehrhardt 1991)	GC	*D. gigas*	Fishes (mainly sardines) are major prey item (47%); crustaceans (20%) and cephalopods (20%) are secondary prey item
(Markaida & Sosa-Nishizaki 2003)	GC	*D. gigas*	Fishes (70%) are major prey item; cephalopods (12.2%) and crustaceans (14%) are minor prey item
(Ruiz-Cooley et al. 2006)	GC	*D. gigas*	Myctophids are major prey; mesopelagic cephalopods and crustaceans (euphasiids) are secondary prey
	IA	*D. gigas*	Large individuals at a higher trophic level than common medium-size ommastrephid squids
Eastern Tropical Pacific			
(Markaida & Hochberg 2005)	GC	Swordfish	Jumbo squid is a major prey item (65%); teleosts are secondary prey (24%); other cephalopods are minor prey (3%)
(Olson & Galván-Magaña 2002)	GC	Dolphinfish	Cephalopods (mainly ommastrephid) are a major prey item (32%)
(Polo-Silva et al.	GC	Common thresher	Cephalopods (mainly jumbo squids and other oceanic squids) are major prey item (84%)

2007)		shark	
(Rosas-Alayola et al. 2002)	GC	Sailfish	Cephalopods (mainly jumbo squids and other oceanic squids) are a major prey item (56%)
Cephalopods			
(Nigmatullin et al. 2001)	GC	Jumbo squid	Wide prey spectrum with crustaceans (amphipods, euphasiids and shrimps), cephalopods (squids and pelagic octopods) and fishes (mainly myctophids)
South Humboldt			
(Clarke & Paliza 2001)	*D. gigas* in GC	Sperm whale	*D. gigas* is a major prey item, other oceanic squids constitute a minor part of ingested mass
(Letelier et al. 2009)	GC	Swordfish	*D. gigas* is the main prey (85%); other oceanic squids (mainly *T. filipovae* are a secondary ite (12%); other cephalopods are absent
(Castillo et al. 2007)	GC	Swordfish	*D. gigas* is a major prey item across all areas (72 to 99%)
(Ibañez et al. 2004)	GC	Swordfish	*D. gigas* (20 to 93%) is a secondary or major prey item and *Onychoteuthis banksia* (2 to 53%) is a minor, secondary or major prey item
(Lopez et al. 2009)	GC	Shortfin mako	Cephalopods (mostly *D. gigas*) are a secondary prey item (12%)
(Lopez et al. 2010)	GC	Blue shark	Cephalopods (mostly *D. gigas*) are a secondary prey item (27%)
(Murillo et al. 2008)	GC	Patagonian toothfish	Cephalopods (mostly oceanic squids) are a minor prey item (1.9%)
(Pardo-Gandrillas et al. 2007)	GC	Juvenile blue shark	*D. gigas* is a secondary prey item (20.7%)
Cephalopods			
(Alarcón-muñoz et al. 2008)	Consumption model	*D. gigas*	Important top-down impact of Jumbo squid on Chilean hake biomass
(Chong et al. 2005)	GC	*D. gigas*	Seasonal variability Cephalopods (54% to 67%) and teleosts (38% to 71%) are a major prey item; crustaceans are minor prey item (1% to 7%)
(Ibáñez et al. 2008)	GC	*D. gigas*	Teleosts (various planktivorous or small carnivorous fishes) are a major prey item; Cephalopods (mainly D. *gigas*) are secondary prey item; crustaceans are minor prey item
(Rosas-Luis et al. 2011)	GC	*D. gigas*	Seasonal variability Fish (mainly myctophids, lightfishes and anchovies) are major prey item (37% to 87%); Cephalopods (mainly *D. gigas*) are secondary or major prey item (12% to 62%); Crustaceans are a minor prey item.
Antarctic			
(Collins &	Review, GC		Various cephalopods species are important prey of seabirds and marine mammals. They are minor prey of

Rodhouse 2006)	and IA		dominating fish family (notothenioids), and a secondary prey of large sharks.
(Rodhouse & White 1995)	GC	Vertebrate predators	Ommastrephids are dominant prey of some species
Cephalopods			
(Collins & Rodhouse 2006)	Review, GC and IA		Wide prey spectrum with fishes (mainly myctophids), crustaceans (mainly euphasiids) and cephalopods
(Rodhouse & White 1995)	GC	Ommastrephids	Myctophids are dominant prey Potentially strong consumption
Atlantic Arctic			
(Bradshaw et al. 2003)	Fatty acids	Sea lion	Squids are a significant prey in summer
(Brown et al. 1999)	Fatty acids	Fur seal	Squids are minor prey
(Chambers & Dick 2007)	GC	49 species	Gonatids are significant prey of predator deep-sea fishes of the system
(Daneri et al. 2000)	Cephalopods in GC	Elephant seal	Squids are the main cephalopod prey, especially *Psychroteuthis glacialis* (81%)
(Gardiner & Dick 2010)	GC	26 predators	Cephalopods (mainly oceanic squid families) are major prey of 10 species; secondary prey of 1 species; minor prey of 15 species
Cephalopods			
(Chambers & Dick 2007)	GC	*G. fabricii*	Wide predation with crustaceans (mainly euphasids and amphipods) and panktivorous or carnivorous fishes
General studies			
(Boyle & Rodhouse 2005)	review	All predators	Cephalopods are prey of seabirds and many large fish species. They also are an important prey of marine mammals.
(Nesis 1997)	Gonatids in GC	Wide spectrum of predators	Significant prey of most top predators of the region (big fishes like mammals), and juvenile cephalopods are an important prey of smaller predators (carnivorous fishes).
(Young et al. 2013)	review	Squids for all predators	Ommastrephids are a major prey of fish predators. Octopods and other pelagic squid families are other important cephalopod prey.
Cephalopods			
(Nesis 1997)	GC	Gonatid squids	Balanced diet between crustaceans (mainly copepods, euphasiids and amphipods), fishes (mainly Myctophids, Microstomatids and juvenile Alaska pollack) and cephalopods (mainly Gonatids)
(Rodhouse & Nigmatullin 1996)	review	All cephalopods	Small crustaceans as juveniles before a shift towards cephalopods and larger fishes. Myctophids are generally the main fish resource

(Barbosa et al. 2008)	review	Squids	Wide trophic spectrum, acting as predators of micronekton as well as top predators

Appendix 2-4. Detailed scores of the various cephalopod functional groups in most adequate models.

Areas and models	Implementation	Groups description	role
Benguela			
Shannon & Jarre-Teichmann 1999	2	Cephalopods	3
Mediterranean Sea			
Barausse et al. 2009	3	Squids	4
		Benthic cephalopods	2
Bay of Biscay			
Lassalle et al. 2011	3	Pelagic cephalopods	2
		Benthic cephalopods	2
North West Atlantic			
Link et al. 2010	3	Cephalopods	2
South West Atlantic			
Gasalla et al. 2010	3	Squids	4
		Octopus	2
South East Australia			
Watson et al. 2013	3	Coastal squids	4
		Transitory squids	4
		Octopus	2
California Current			
Field et al. 2007	3	Cephalopods	4
Eastern Tropical Pacific			
Field et al. 2007	3	Cephalopods	4
South Humboldt			
Arancibia & Neira 2008	3	Jumbo squid	3
		Other cephalopods	2
Antarctic Peninsula			
Cornejo-Donoso & Antenaza 2008	2	Squids	1
Bay of Bengal			
Ullah et al. 2012	2	Cephalopods	1
Atlantic Arctic			
Pedersen & Zeller	2	Squids	1
North West Pacific			
Zhang et al. 2007	2	Cephalopods	4

Appendix 2-5. Comparison between scores obtained from the review and the local experts feedbacks.

Areas and models	Our scores Data quality / Role	Expert scores Data quality / Role
Benguela		
Shannon & Jarre-Teichmann 1999	2/2	2/3
Bay of Biscay		
Lassalle et al. 2012	3/2	2/2
North West Atlantic		
Link et al. 2010	3/2	3/2
Bay of Bengal		
Ullah et al. 2012	2/3	2/1
Atlantic Arctic		
Pedersen & Zeller	2/2	1/1

Appendix 3-1: identification of cephalopod species and groups from predator diets (in percentage of diet weight). Boxes in yellow are values above 5%, highlighting the predators for which cephalopod species represent a substantial part of the diet.

		Ceph % in diet (weight)		N. gouldi	T. eblanae	O. bartramii	Other oceanic squid	Octopods	cuttlefishes	neritic squid	architeuthis	O. robsoni	References.	Method used
Toothed whales	sperm whale	100.00		3.33	8.67	0.53	18.93	7.33	0.00	0.00	18.00	43.20	(Evans & Hindell 2004)	gut content
Epipelagic large piscivores	yellowfin Tuna	7.00		0.19	0.86	0.30	5.50	0.15	0.00	0.00	0.00	0.00	(Lansdell & Young 2007; Young et al. 2010)	gut content
	bluefin	26.00		12.00	1.00	0.00	13.00	0.00	0.00	0.00	0.00	0.00	(Young et al. 1997; Young et al. 2010)	gut content
Mesopelagic large piscivores	swordfish	80.00		22.90	0.90	28.70	27.50	0.00	0.00	0.00	0.00	9.52	(Lansdell & Young, 2007; Young et al. 2010)	gut content
Pinnipeds	fur seal	11.40		6.80	0.00	0.00	0.00	4.60	3.30	0.30	0.00	0.00	(Deagle et al. 2009; Hume et al. 2004)	feces and regurgitates DNA
gummy shark	gummy shark	49.54		6.09	0.00	0.00	6.52	36.94	0.00	0.00	0.00	0.00	(Coleman & Mobley 1984)	gut content
demersal sharks	whiskery shark	93.87		16.13	0.00	0.00	0.00	77.74	0.00	0.00	0.00	0.00	(Coleman & Mobley 1984)	gut content
pelagic shark	school shark	81.36		11.95	0.00	0.00	0.00	69.40	0.00	0.00	0.00	0.00	(Coleman & Mobley 1984)	gut content
deep demersal fish	toothed whiptail	11.34		0.00	0.00	0.00	0.00	11.34	0.00	0.00	0.00	0.00	(Coleman & Mobley 1984)	gut content
shallow demersal	john dory	1.54		1.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	(Coleman & Mobley 1984)	gut content
flathead	toothy flathead	68.00		16.76	0.00	0.00	0.00	51.24	0.00	0.00	0.00	0.00	(Coleman & Mobley 1984)	gut content
shallow piscivore	Yellowtail kingfish	50.00			0.00	0.00	0.00	50.00	0.00	0.00	0.00	0.00	(Coleman & Mobley 1984)	gut content
	dolphinfish	8.00		0.68	5.84	0.68	0.10	0.70	0.00	0.00	0.00	0.00	(Lansdell & Young, 2007; Young et al. 2010)	gut content

T. eblanae, O. bartramii and Onykia robsoni were only significant source of food (>5% of the diet) for one or two predators that are part of larger groups (sperm whales part of toothed whales, swordfish part of large piscivores 2, dolphinfish part of shallow piscivore). We thus decided to group them in a single group of oceanic squids.
Architeuthis are not included in the model as their appearance in the region is relatively scarce and they are preyed upon by very few top predators.
Cuttlefishes and neritic squids do not seem to be an important source of food for predators where specification was available (they never represent more than 5% of the diet). However, we kept them in separate groups due to their different ecology and their respective interest for fisheries.

Appendix 3-2a: origin of base parameters.

	Distribution	Abundance	Main trophic links	Movement	Reproduction	Fisheries catch range (2000-2013)	Environmental sensitivity
arrow squid (*N. gouldi*)	(Stark 2008)	(Stark 2008, www.fish.gov	See appendix 1	(Stark 2008)	(Jackson et al. 2005; Green 2011; Stark 2008)	(www.fish.gov)	(Green 2011)
	(Nowara & Walker 1998; Uozumi 1998; Reid 2016)		(Braley et al. 2010; Pethybridge et al. 2012)		(Jackson et al. 2005; Virtue et al. 2006)		
Oceanic squids (*O. bartramii*)	(Dunning & Brandt 1985)		See appendix 1	(Bower & Ichii 2005)	(Ichii et al. 2004; Nishikawa et al. 2014; Vijai et al. 2014) (NW_Pacific)	(www.fish.gov)	(Chen & Chiu 2003) (NW_pacific)
	(Bower & Ichii 2005; Watanabe, Tsunemi Kubodera, et al. 2004; Reid 2016)		(Parry 2003; Watanabe, Tsunemi Kubodera, et al. 2004)				
calamari (*S. australis*)	(Pecl et al. 2006; Steer et al. 2007)		See appendix 1	(Pecl et al. 2006)	(Jackson et al. 2003; Moltschaniwskyj & Pecl 2007; Pecl et al. 2004; Pecl 2001; Steer et al. 2007)	(www.fish.gov)	(Moltschaniwskyj 2004; Pecl 2004; Pecl 2001)
	(Triantafillos 2002)						
Giant cuttlefish (*S. apama*)	(Hall & Hanlon 2002)	(Hall & Fowler 2003)	See appendix 1	(Aitken et al. 2005)	(Hall & Fowler 2003)		(Domingues et al. 2002) (*Sepia officinalis*)
	(Hall & Fowler 2003)						
Pale octopus (*O. pallidus*)	(Leporati et al. 2008)		(Smith 2003) (*O. vulgaris*)		(Leporati et al. 2008)		(André et al. 2009)
Gloomy octopus (*O. tetricus*)	(Ramos et al. 2015)		See appendix 1		(Ramos et al. 2015; Hart et al. 2016)		(Ramos et al. 2014)
	(Anderson 1997; Ramos et al. 2015)		(Hart et al. 2016, Smith 2003) (*O. vulgaris*)				

Note: many references are used as base but often completed by other cited references (i.e. distributions can be or movements can be looked at through diet studies etc…)
Many parameters of the oceanic squid groups come from Ommastrephid species, as they have been the subject of many studies in the North West Pacific; and it's relatively high abundance means it has high fisheries exploitation potential (Dunning & Brandt 1985).

Appendix 3-2b: Origin of parameters of cephalopods and methods of analysis used

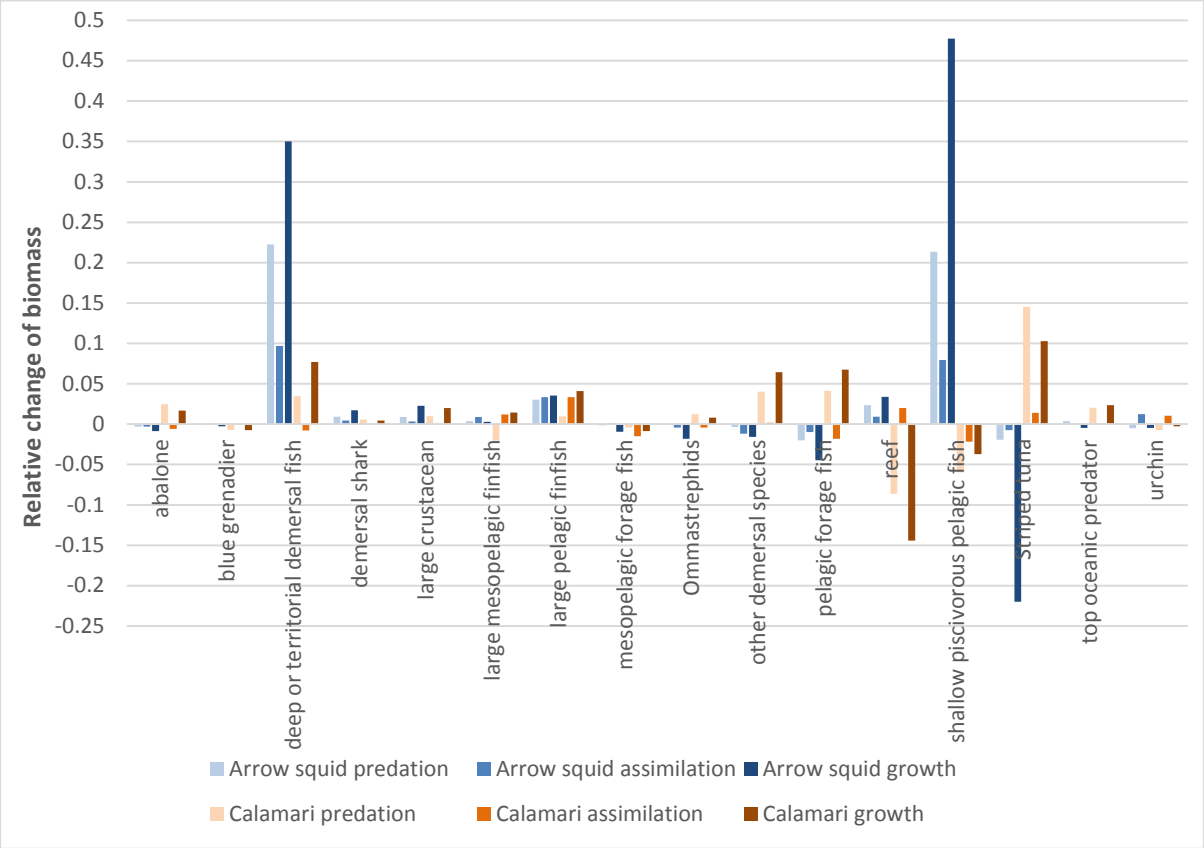
parameter	species	References **Local**/foreign	Database and information	balancing
Abundance and horizontal distribution	*N. gouldi, S. australis* and *O. pallidus*	**www.fish.gov** **…**	CPUE of fisheries, surveys and predators diet	Abundance estimated through calibration
	S. apama	**Triantafillos (2002)**	Biomass estimation on spawning aggregation	Abundance estimated through calibration
	Ommastrephids *O. tetricus*	**Lansdell & Young (2007)**	From relative abundance in predators diet and squid catches	Abundance estimated through calibration
Vertical distribution	*N. gouldi*	**Nowara & Walker (1998)** Uozomi (1998)	Surveys Fisheries sampling	
	Ommastrephids	Bower & Ichii 2005, Watanabe et al. 2004	Surveys Surveys and Fisheries sampling	
	S. australis	**Triantafillos (2002)**	Survey	
	S. apama	**Hall & Fowler 2003**		
	O. pallidus	**Leporati et al. 2008a**	Survey	
	O. tetricus	**Anderson 1997**	Survey	
maturity	*N. gouldi* Ommatrephids *S. australis* *S. apama* *O. pallidus* *O. tetricus*	**Jackson & McGrath-Steer-2002, Green 2011, McGrath & Jackson 2002** Yatsu et al. 1997, Bower & Ichii 2005, Vijai et al. 2014 **Triantafillos 2002, Steer et al. 2007** **Hall & Fowler 2003** **Leporati et al. 2008** **Hart et al. 2016, Ramos et al. 2014**	Body weights, weights of reproductive apparatus and maturation stages	
Growth and temperature sensitivity	*N. gouldi* *O bartramii*	**Jackson et al. 2003,** Chen & Chiu 2003	Statolith formation	
	S. australis	**Triantafillos 2002, Pecl 2004**	Cuttlebone formation	
	S. apama *O. pallidus* *O. tetricus*	**Hall & Fowler 2003, Leporati et al. 2008, Ramos et al. 2014, Hart et al. 2016**	Stylets formation	
Clearance rate (maximum search	*N. gouldi* *S. australis*	**Stark et al. 2005** **Pecl et al. 2006**	Tag and isotope tracking	

volume)	others			Clearance estimated through calibration
Availability matrix	*N. gouldi*	**Braley et al. 2010** **Pethybridge et al, 2012**	Gut content DNA Gut content, lipid and fatty acid analysis	Will be balanced so the initial diet resulting from the model matches the observed diet
	Ommastrephids	Bower & Ichii 2005	gut contents	
	other	Rodhouse & Nigmatullin 1996	Gut content	
assimilation			General review	
recruitment				Through calibration

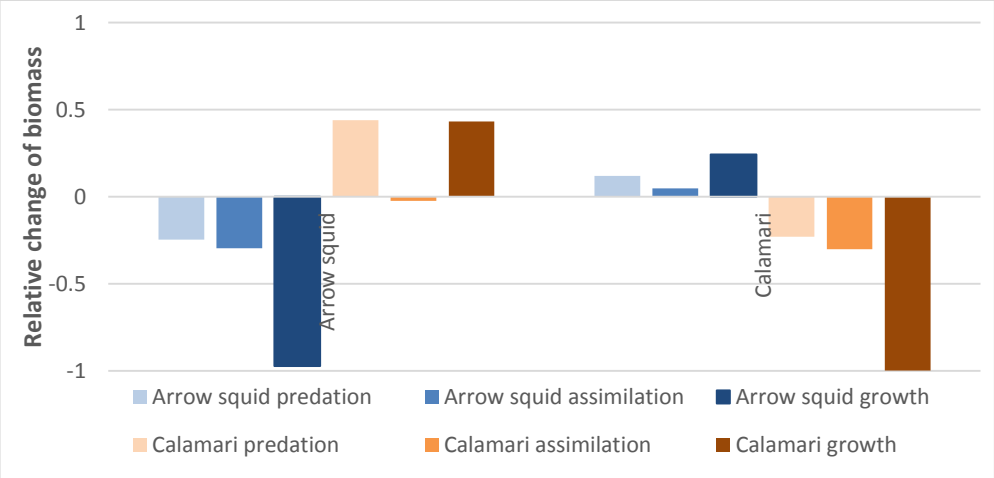
Appendix 3-3: results of the PCA analysis that allowed us to gather functional groups that were impacted in similar ways by our tests in larger ensembles.

grp	large_group	Comp.1	Comp.2
FPL	pel1	-0.14038	-0.1952
FBG	mesopel2	0.040998	0.264989
FPS	pel1	-0.09896	-0.13014
FVD	pel2	0.185003	-0.16045
FBM	reef1	0.185341	0.079881
FVS	pel1	-0.15828	-0.04286
FDR	reef1	0.200967	0.146719
FTE	pred5	0.041465	0.045135
FTM	pred4	-0.02102	0.172299
FMM	mesopel1	-0.01422	0.011707
FMN	mesopel1	-0.1229	0.16064
FBP	reef1	0.155263	0.146751
FDD	dem1	0.126973	-0.22427
FDS	dem2	-0.21101	-0.09805
FDM	reef2	0.048844	-0.16162
FDT	dem1	0.176603	-0.13501
FBW	reef2	0.019011	-0.0831
FSN	reef1	0.201289	0.078722
FWT	reef1	0.139741	0.126899
FST	pred3	-0.20262	0.161638
SHG	pred2	0.061763	-0.283
SHD	pred2	0.148054	-0.23648
SHS	pred1	-0.04078	-0.19137
SHP	pred1	-0.21605	-0.10582
SHR	pred1	-0.17364	-0.19401
SSK	dem2	-0.23072	-0.03669
SB	bird	-0.20582	0.02107
BGU	crust3	-0.02708	0.092423
PIN	pred1	-0.22643	-0.06035
BGA	crust2	-0.19342	-0.12827
WHB	baleens	-0.23735	0.055753
WHS	pred1	-0.24	-0.03088
WHT	pred1	-0.19418	-0.13277
BRL	crust1	0.053388	-0.28913
NGO	arrow squid	-0.20176	0.143237
OMM	Ommastrephids	-0.21995	0.115345
SQN	calamari	0.197513	0.072876
BFF	filter feeder	-0.02964	0.172157
BFD	filter feeder	-0.09501	-0.02058
BMD	crust1	0.094141	-0.2711
BMS	crust1	0.072663	-0.2833
ZL	plankton	0.018045	-0.10895

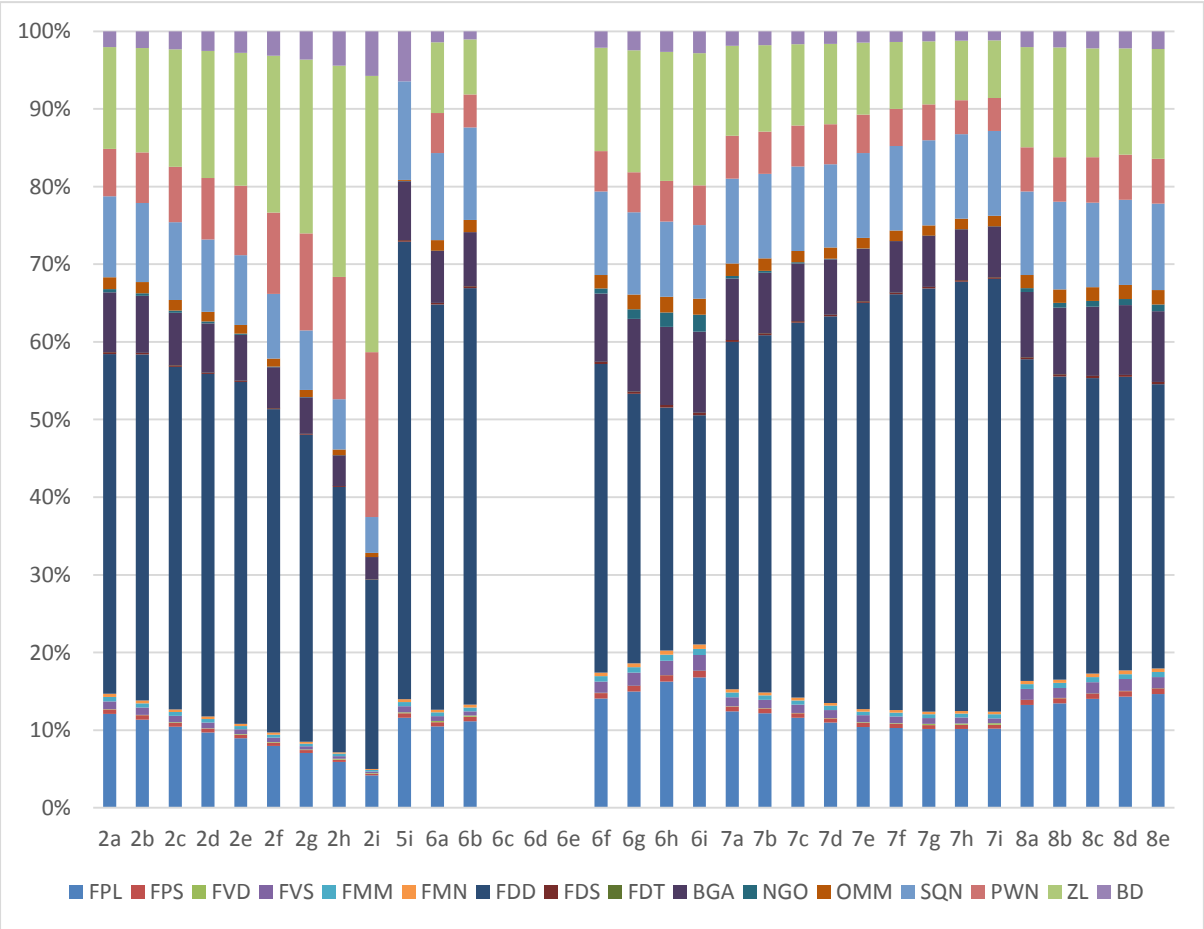
Appendix 3-4a: comparison of the impacts on the food web of tests on arrow squid and calamari. These effects are displayed using the relative change of biomass of groups compared with our base run.



Appendix 3-4b: effects of various tests on arrows squid and calamari. The results of the tests on arrow squid are given in blue, the results of the tests on Calamari in brown. This is simply evidence that we compared results of tests with similar changes on tested species (i.e. results of tests on arrow squid are from abundance reductions of a similar degree to those in the tests on calamari) – more information on this is given in appendix 3-4a.



Appendix 3-5: Diets of adult arrow squid at the end of each test. Missing columns are from scenarios where the arrow squid abundance was depleted.



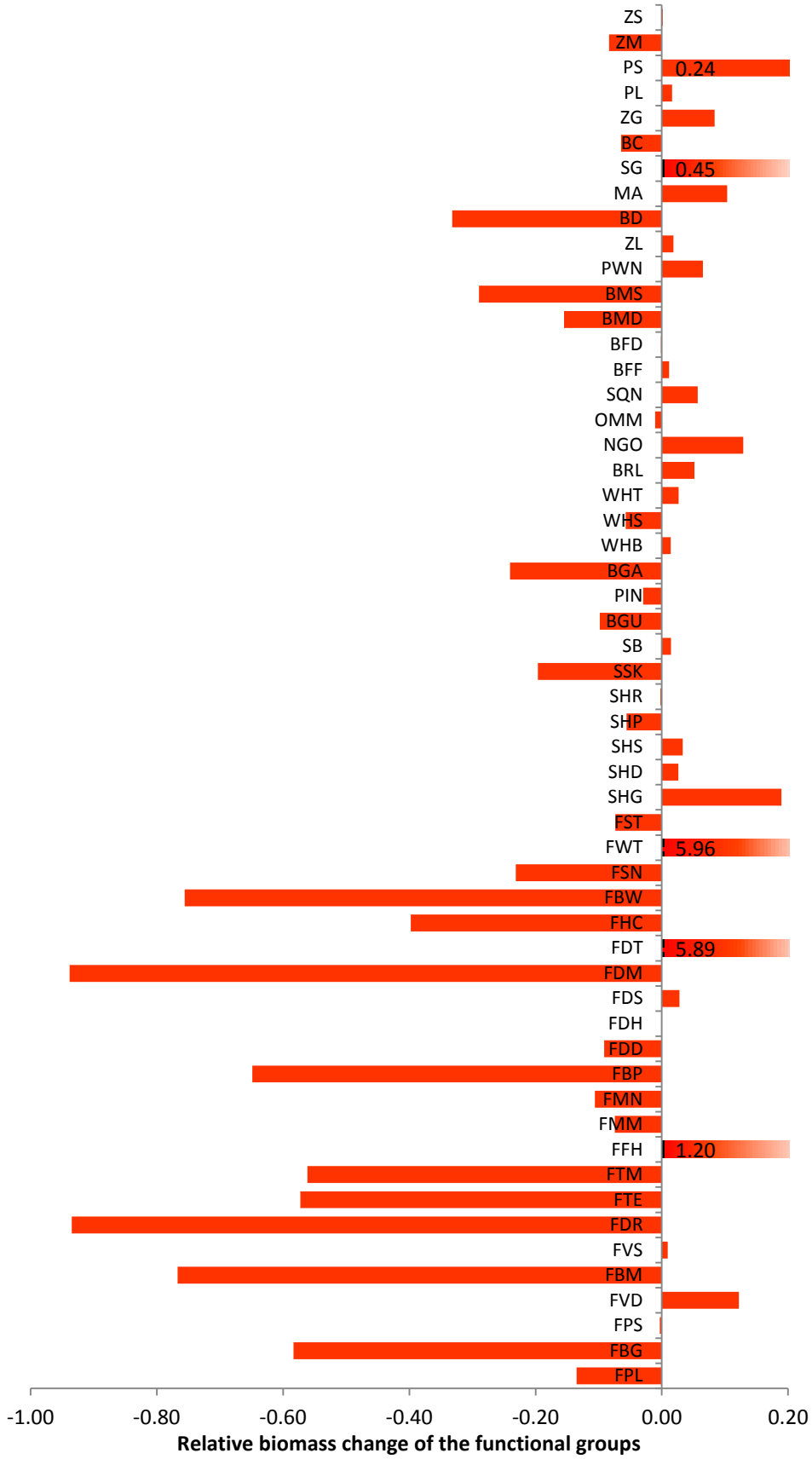
Appendix 4-1: Cephalopod groups and parameterization of their sensitivity to environmental changes.

species	Note on Temperature-Growth relationship strength	optimum temperature (maximum-minimum)
N. Gouldi	Relatively weak	17 (24-8)
Ommastrephids	Weak	19 (21-7)
S. australis	Strong relationship	22 (24-8)
S. apama	Relatively strong	18
O. pallidus	Relatively strong	16.5 (23-12)
O. tetricus	Strong relationship	23 (25-15)

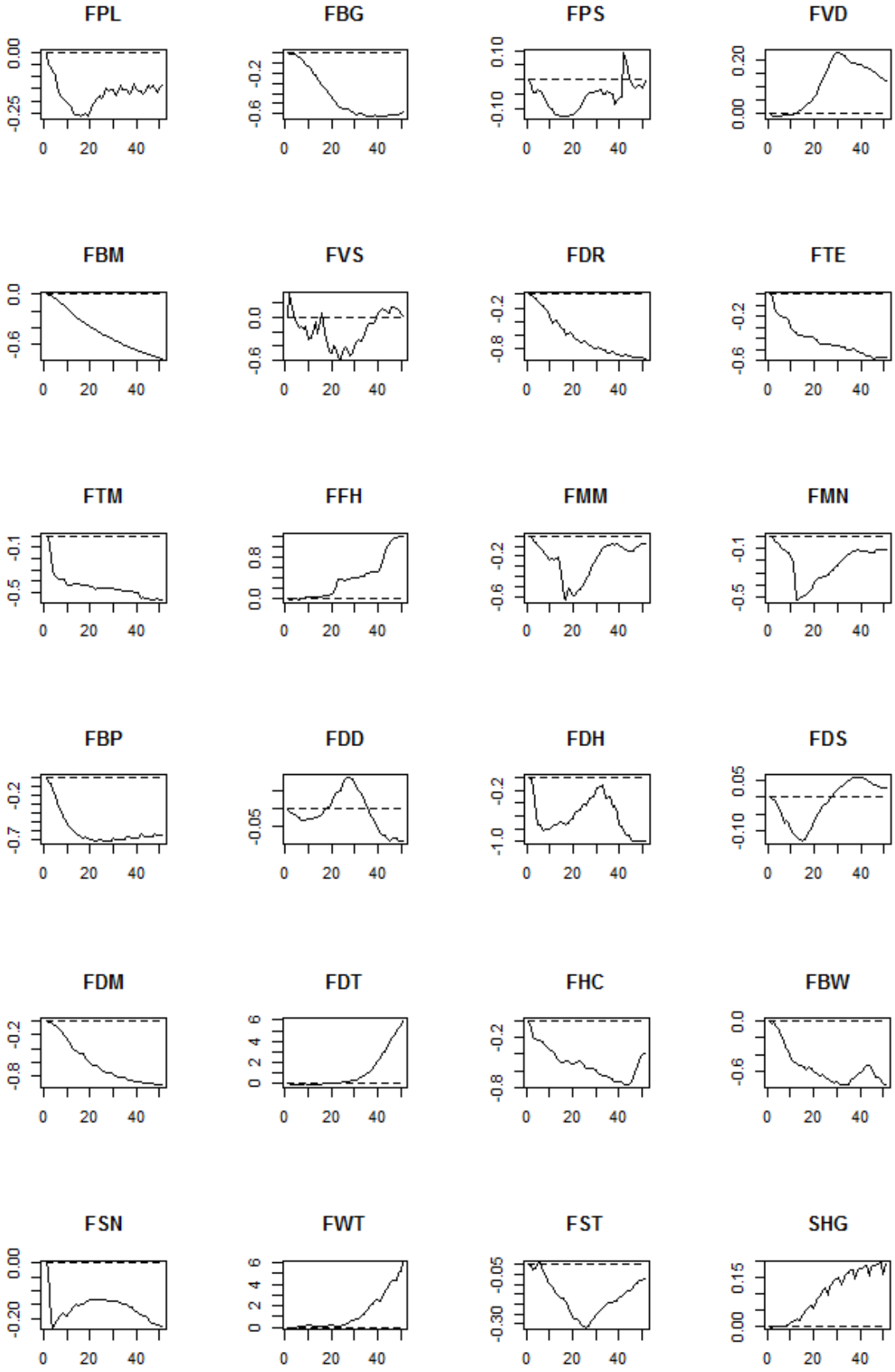
Appendix 4-2: cephalopod groups and parameterization of their sensitivity to environmental changes, sources.

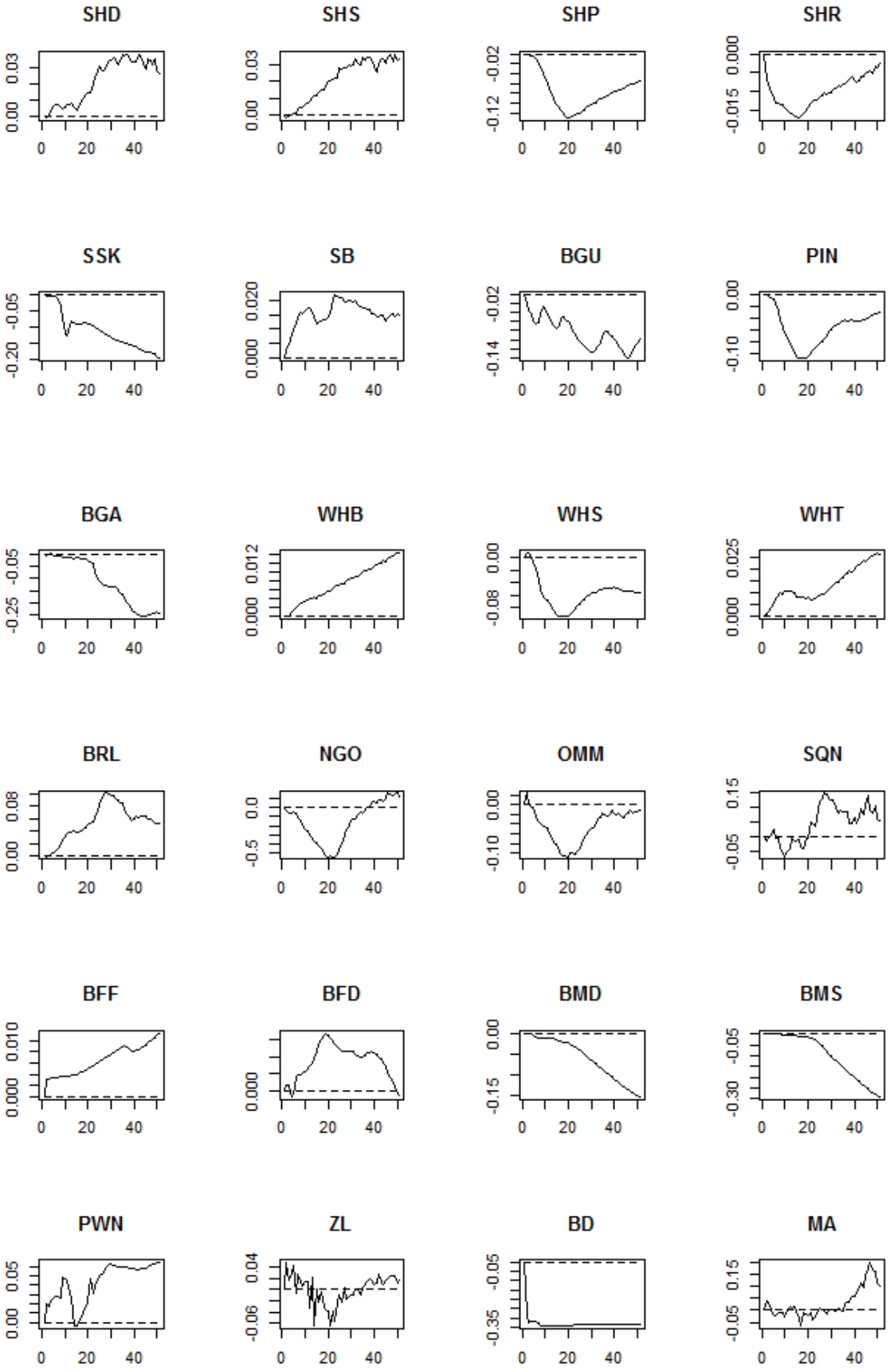
species	sources
N. Gouldi	(Green 2011; Stark 2008; Watanabe et al. 2006)
Ommastrephids	(Ichii et al. 2004)
S. australis	(Pecl & Moltschaniwskyj 2006; Steer et al. 2007; Triantafillos 2002)
S. apama	(Hall & Fowler 2003; Payne et al. 2011)
O. pallidus	(André et al. 2009)
O. tetricus	(Joll 1977)

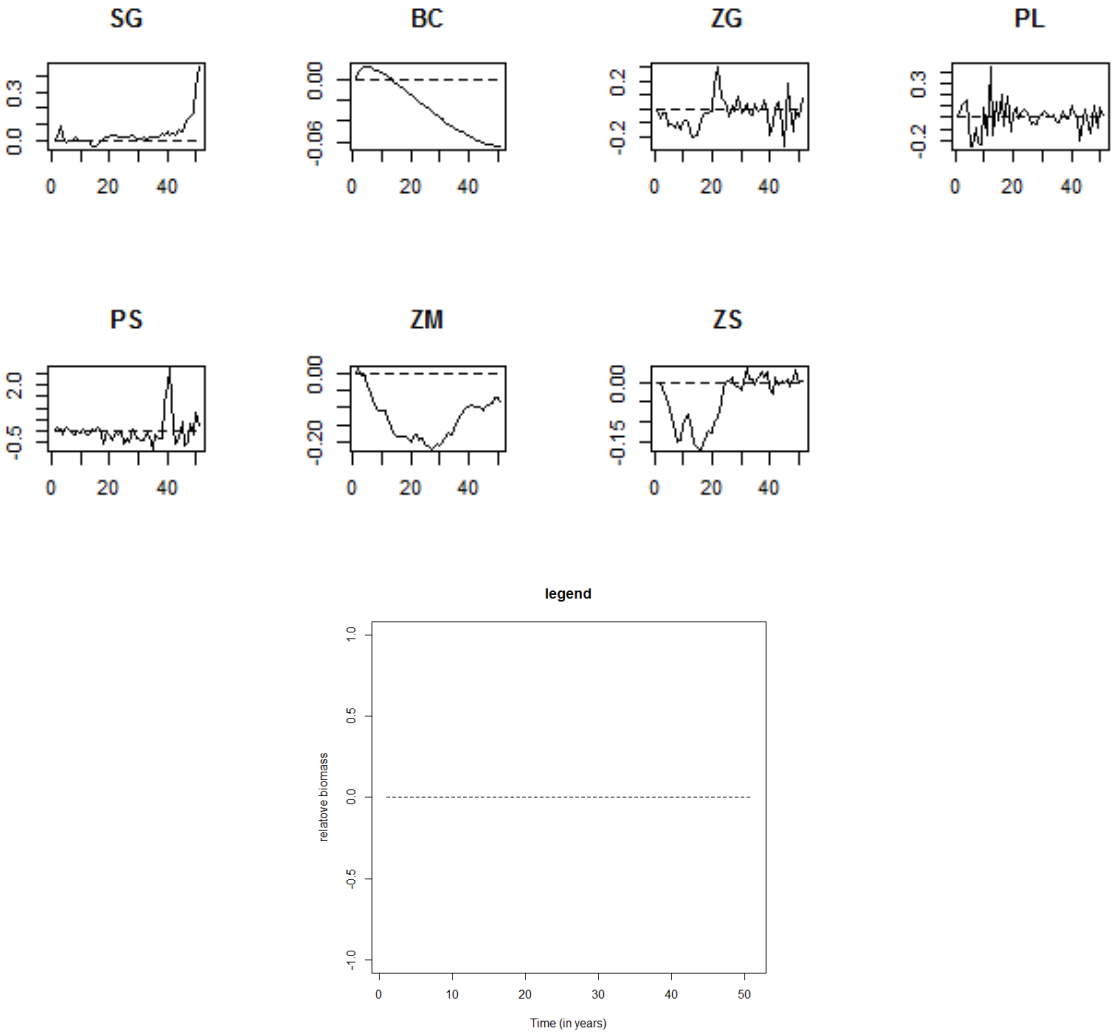
Appendix 4-3: Relative biomass change at the end of the 50 years RCP8.5 scenario. The upper limit of the biomass change axis has been limited in order to make the figure easier to read. Labels with the value of the change were associated to groups with a biomass change too great to be displayed.



Appendix 4-4: Relative biomass changes of all the groups through the 50 years of increasing temperature.




SHD
SHS
SHP
SHR
SSK
SB
BGU
PIN
BGA
WHB
WHS
WHT
BRL
NGO
OMM
SQN
BFF
BFD
BMD
BMS
PWN
ZL
BD
MA


SG
BC
ZG
PL
PS
ZM
ZS
legend
relative biomass
Time (in years)

Appendix 4-5: Biomass changes after the 60 years.

-0.6 and lower		-0.2 to -0.6		-0.2 to 0		0 to +0.2		+0.2 to +0.6		+0.6 and higher	
6 groups		8 groups		17 groups		19 groups		2 groups		3 groups	
FDH	-1.00	FBG	-0.58	SSK	-0.20	ZS	0.00	PS	0.24	FFH	1.20
FDM	-0.94	FTE	-0.57	BMD	-0.15	FVS	0.01	SG	0.45	FDT	5.89
FDR	-0.93	FTM	-0.56	FPL	-0.13	BFF	0.01			FWT	5.96
FBM	-0.77	FHC	-0.40	FMN	-0.11	WHB	0.01				
FBW	-0.76	BD	-0.33	BGU	-0.10	SB	0.01				
FBP	-0.65	BMS	-0.29	FDD	-0.09	PL	0.02				
		BGA	-0.24	ZM	-0.08	ZL	0.02				
		FSN	-0.23	FMM	-0.07	SHD	0.03				
				FST	-0.07	WHT	0.03				
				BC	-0.06	FDS	0.03				
				WHS	-0.06	SHS	0.03				
				SHP	-0.06	BRL	0.05				
				PIN	-0.03	SQN	0.06				
				OMM	-0.01	PWN	0.06				
				FPS	0.00	ZG	0.08				
				SHR	0.00	MA	0.10				
				BFD	0.00	FVD	0.12				
						NGO	0.13				
						SHG	0.19				

Demersal vertebrate species
Oceanic species vertebrate species
Crustaceans and filter feeders
Squid species
Primary and secondary producers
Seabirds

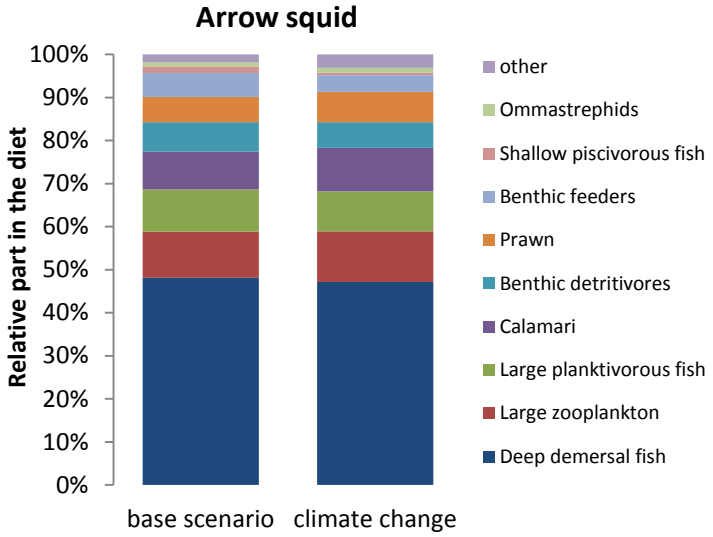
Appendix 4-6a: relative importance of prey groups in diets of the various squid groups in our two scenarios (table).

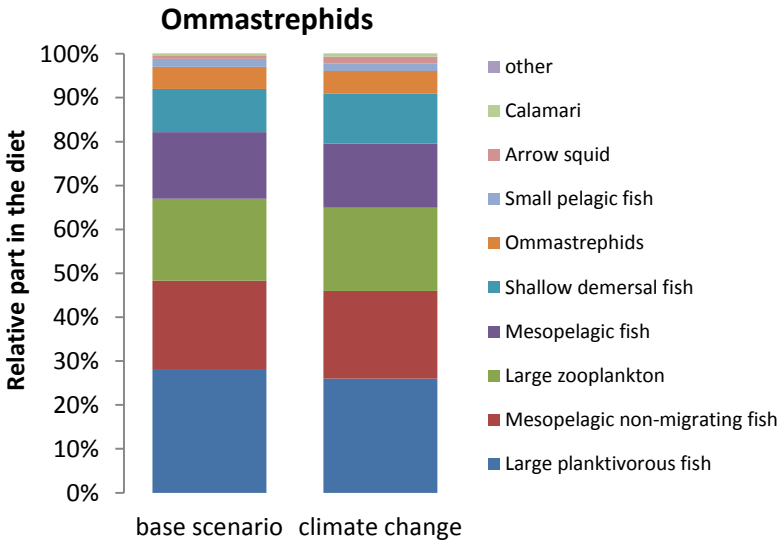
	arrow squid	
Prey groups	Base	climate change
Deep demersal fish	0.48	0.48
Large zooplankton	0.11	0.12
Large planktivorous fish	0.10	0.09
Calamari	0.09	0.10
Benthic detritivores	0.07	0.06
Prawn	0.06	0.07
Benthic feeders	0.06	0.04
Shallow piscivorous fish	0.01	0.01
Ommastrephids	0.01	0.01
other	0.02	0.03

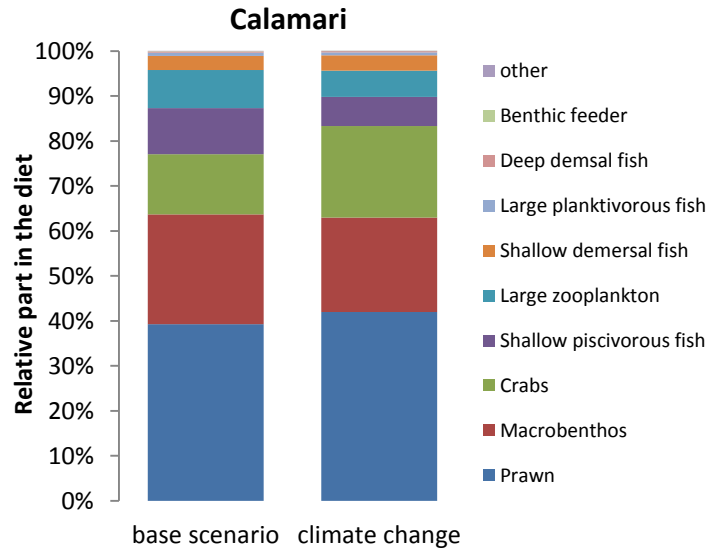
	ommastrephid	
Prey groups	base	climate change
Large planktivorous fish	0.28	0.26
Mesopelagic non-migrating fish	0.20	0.20
Large zooplankton	0.19	0.19
Mesopelagic fish	0.15	0.15
Shallow demersal fish	0.10	0.11
Ommastrephids	0.05	0.05
Small pelagic fish	0.02	0.02
Arrow squid	0.01	0.02
Calamari	0.00	0.01
other	0.00	0.00

	calamari	
Prey groups	base	climate change
Prawn	0.39	0.42
Macrobenthos	0.24	0.21
Megazoobenthos	0.13	0.20
Shallow piscivorous fish	0.10	0.06
Large zooplankton	0.08	0.06
Shallow demersal fish	0.03	0.03
Large planktivorous fish	0.01	0.01
Deep demersal fish	0.00	0.00
Benthic feeder	0.00	0.00
other	0.00	0.00

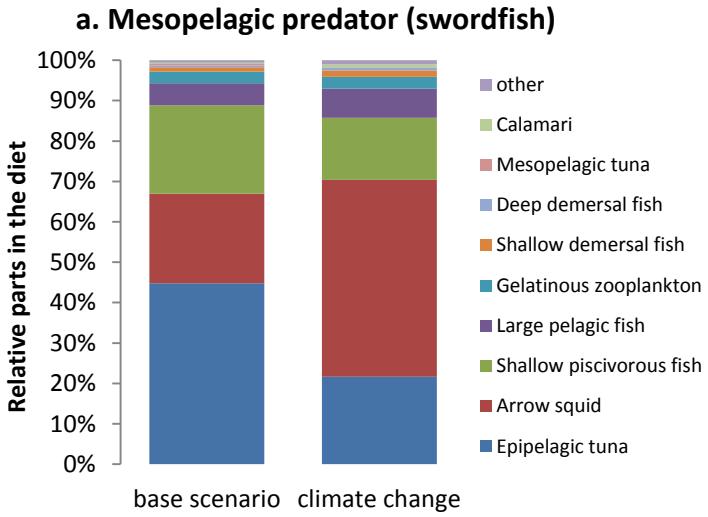
Appendix 4-6b: relative importance of prey groups in diets of the various squid groups in our two scenarios (figures).

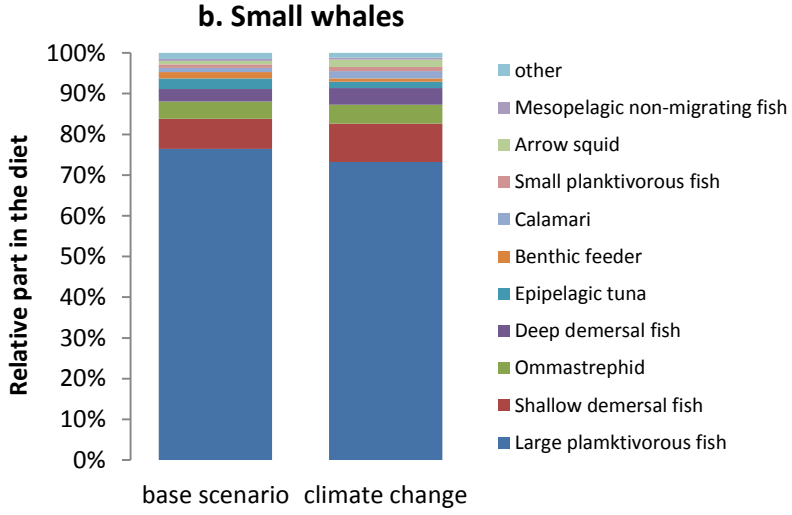


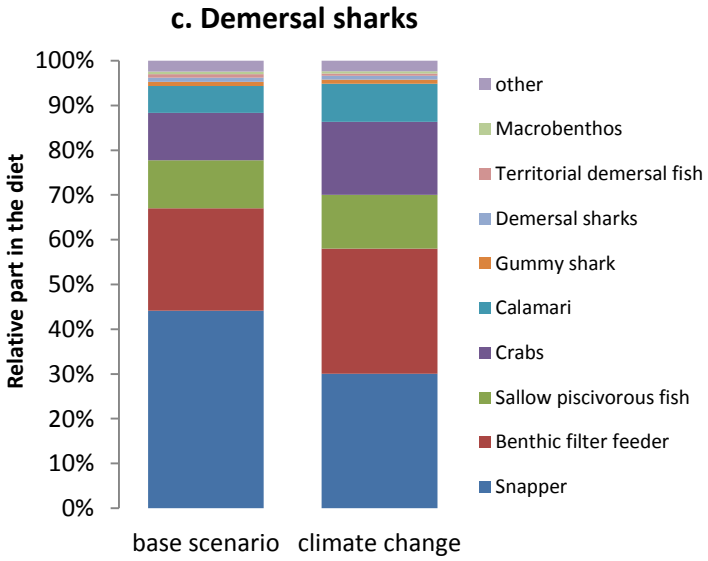




Appendix 4-7: Relative importance of prey groups in the diet of the main predator of arrow squid (a), ommastrephid (b) and calamari (c). These predators are the ones with the highest portion of arrow squid, ommastrephid and calamari respectively in their diet.







Appendix 4-8: Physiological condition differences of the various squid species at the end of the standard scenario and climate change scenario.

	Weight change after 50 years of temperature increase	Change in the reserve/structure ratio
Arrow squid	-3.26%	-0.2%
Calamari	-6.58%	-0.1%
Ommastrephid	-5.13%	-0.01%

The weight changes displayed here are from the heaviest individuals of each species.

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